AN INTRODUCTION TO THE STUDY OF FOSSILS

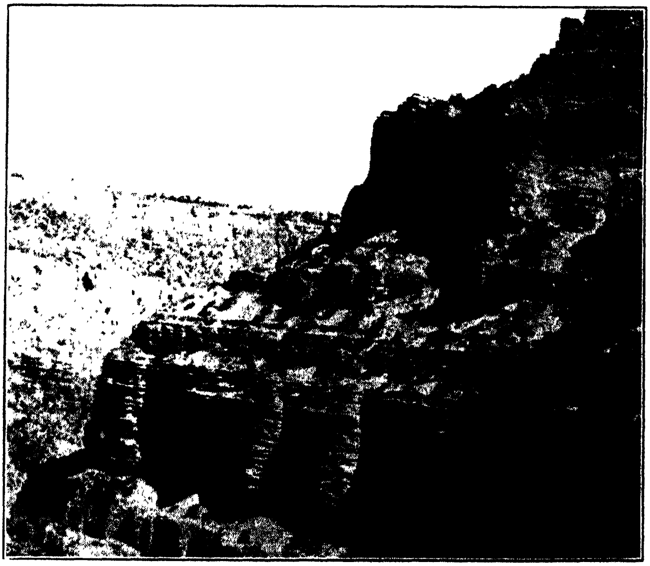
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Low tide on the Atlantic coast at Cohasset, Massachusetts. Here shells and seaweed are being buried, the first step in becoming fossils.



Paleozoic strata in the canyon of the North Platte river. These are deposits that were laid down in the ocean covering Wyoming during parts of the Paleozoic, and in them are the fossilized remains of the life of those ancient seas.

SEA BEACHES, MODERN AND ANCIENT

AN INTRODUCTION TO THE STUDY OF FOSSILS

(PLANTS AND ANIMALS)

BY

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TO

MY WIFE

COMRADE AND COLLABORATOR

THIS BOOK

IS DEDICATED

PREFACE TO THE SECOND EDITION

In the preparation of the revised edition, the author has retained the primary aim of awakening interest in paleontology as the study of once living organisms. He hopes that the student may thus be helped to regard fossils, not merely as isolated, interesting phenomena, or even as very old relatives of living forms, but as plants or animals living their lives in their ancient environments just as plants and animals are doing to-day.

As in the former edition, the fossils are interpreted through the structure, physiology, and ecology of related living forms. It has been the endeavor to bring the classification of both plants and animals into line with the conclusions of the majority of workers in the various fields. Summaries of the relationship and evolution of phyla and classes have been added in accordance with the most widely accepted interpretations, and the contributions of each phylum as rock-builders have been summarized. The introductory chapter on general considerations has been much enlarged.

The author is indebted to various persons for aid in this revision; he particularly wishes to acknowledge his debt to Dr. Charles Blake of the Massachusetts Institute of Technology, also to Professor B. F. Howell of Princeton University, and to Dr. Louis Hussakof of the American Museum of Natural History.

H. W. S.

Cambridge, Massachusetts
August, 1933

PREFACE TO THE FIRST EDITION

This little volume has grown out of a need experienced by the author during fifteen years of teaching paleontology. He has found that students come to the subject either with very little previous training in biology, or at best with a training which has not been along the lines that would definitely aid them in understanding fossils. Too often fossils are looked upon merely as bits of stone, differing only in form from the rocks in which they are embedded. Hence to awaken interest in them as once living animals and plants, connected by the wonderful chain of evolution with the animals and plants now living, has been the chief aim of the author's lectures and laboratory work upon introductory paleontology which he here presents.

To this end certain living forms have first been discussed as types of their phyla or classes with especial reference to those features which will help the student to understand the related fossil forms considered later. The response which these living forms make to their environment is considered, where they live, how their life is maintained, and how they perpetuate their kind. The relation of the soft body to the hard skeleton or shell is especially emphasized, since it is largely through this very intimate relationship that our interpretation of extinct life is made possible. The student may thus reconstruct from the hard parts preserved in the rocks the appearance of the once living animal. The discussion has been kept as free as possible from unnecessary technical terms.

Beyond this work of showing how past life may be interpreted by the life of the present, and beyond this first comprehensive view of the animal and plant world, such a book as this need

not go. For further and more detailed study of the fossils themselves other books furnish ample material.

The author is indebted to many persons for aid in the preparation of this volume, and in particular wishes to express his gratitude to the following for criticism of various portions of the manuscript and for the loan of illustrations:

R. S. Bassler of the United States National Museum, Louis Hussakof of the American Museum of Natural History, Gary N. Calkins and Amadeus W. Grabau of Columbia University, John M. Clarke and Rudolph Ruedemann of the New York State Geologic Survey, Charles Schuchert and Richard S. Lull of Yale University, Percy E. Raymond and William F. Clapp of the Museum of Comparative Zoölogy, Harvard University, Francis N. Balch of Boston, Robert T. Jackson and Joseph A. Cushman of the Boston Society of Natural History, Charles H. Warren and R. P. Bigelow of the Massachusetts Institute of Technology, Edward S. Morse of the Peabody Academy of Science, Salem, and S. W. Williston of Chicago University.

To G. R. Wieland of Yale University he feels especially indebted for most valuable suggestions on, and the loan of illustrations for, the chapter on plants. The original drawings in the book owe much to the scientific knowledge and personal interest which their delineator, Mr. J. Henry Blake of Cambridge, has contributed to their execution.

H. W. S.

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CHAPTER I

GENERAL CONSIDERATIONS

From living form to fossil. — A walk along a seashore is a walk through one of nature's more interesting laboratories. Forces organic and inorganic are obviously at work, processes of unending change are going on under our eyes. The shore line is being torn down here and being built up there. Myriads of small sea creatures cling to the rocks or burrow in the sand; the empty shells of myriads of others have been swept up on the beach where we see them half buried by the sand as it is washed up by the waves. Among these native inhabitants of the shore are occasional sponges that have been torn away from their deeper water habitat, bones of fish from farther out in the ocean, and occasional fragments that tell of the life of the adjoining land. Little by little these ill-assorted remains of life, the harder and hence the more enduring parts of the organism, whether shell or skeleton, are buried by the sand. Thus they enter the first stage of becoming fossils.

We may suppose the sea beaches of the ancient periods of earth history to have been laboratories of cliff erosion and of shore building, of animal life and of the burial of their remains. Slabs of ancient rocks preserve the wave and ripple marks of the beaches of which they are a hardened fragment, as well as the petrified shells of their inhabitants.

Conditions of preservation. — 1. The organism must escape immediate disintegration. Only a very small proportion of

living forms are preserved. We have seen that the first condition of fossil formation is that the shell or bone soon becomes embedded in some protective material. Otherwise it becomes disintegrated under the mechanical and chemical attacks of rain and wave. The remains of land animals and plants have a much smaller chance of preservation than marine forms. As we look upon the land life around us — grasses, asters and goldenrods, leaves of trees, rabbits, insects, and snakes — we realize that these forms usually die and disintegrate in the locality where they have lived. Such comparatively rare specimens as survive this destruction are rubbed and worn and broken in their passage downstream to lake or ocean and are ground to pieces by the waves if they are deposited in shallow water. If some in many millions happen to settle in deeper water, they are attacked by bacteria, fungi, and animal scavengers unless quickly protected by a thick coating of sediment. Even after burial they are subject to bacterial and chemical disintegration.

2. The plant or animal must be covered by some protective material.

The habitat of the animal determines the kind of protective material in which it may become embedded after death. Such protective materials include sedimentary deposits due to water or wind, ashes from volcanic explosions, bog waters, resin, ice, and incrustations from mineral solutions.

Occasionally the entire animal or plant is encased by the rapid deposition of silica, or of calcium carbonate. Such incrustations may occur through immersion in springs, as in the geyser area of the Yellowstone National Park. Much more common is preservation by means of water which has percolated through or over limestone beds; upon the evaporation of the water the lime which it had dissolved is again deposited. This is especially apt to occur in caves or at the margins of limestone ledges. Many remains of Pleistocene man and beast occur in caves of western Europe preserved by such a stalagmite covering.

During a time of increasing cold, as at the beginning of the

late Glacial Period, the bogs within the colder areas became frozen. In these natural refrigerators remains of plants and animals are well preserved.

As resin stickily exudes from trees it is apt to hold all small objects that touch it, especially seeds and insects, and these are soon completely inclosed by it. Fossil resin, known as *amber*, is found in various parts of the world, but is most abundant in the Oligocene beds along the Prussian shores of the Baltic Sea.

The water of peat bogs and marshes has antiseptic properties, and because of this organisms immersed in it decay very slowly. Logs long inclosed in such waters have been dug up and utilized in various regions, such as southern New Jersey.

Volcanic eruptions are at times accompanied by very much fragmental material, especially ash. If this happens to fall thickly into a shallow lake it carries down with it the leaves and dead insects floating on the surface. Such showers occurred at times during the Miocene at Florissant in Colorado, and to them we doubtless owe much of the marvelous record of insect life there preserved (Fig. 168).

Similarly, when prevailing winds blow from a dry into a moist region, or from an area without vegetation into one with it, dust will accumulate in the latter region, resulting in time in thick deposits of unconsolidated, fine, porous, siliceous silt. Such deposits, called *loess*, are especially abundant in North America, Europe and Asia, from Pleistocene times to the present; they frequently contain land shells. Some loess is of aqueous origin. The coarser wind deposits, such as sand dunes, are not likely to contain fossils; such an unfossiliferous dune deposit is seen in the coarse-grained, white sandstone (Navajo formation) of Jurassic age in southern Utah.

The vast majority, however, of organic remains preserved as fossils have been covered with sediment brought by water. Deposits upon the surface of the continent — lake, flood plain, alluvial-fan, and playa deposits — are in the zone where erosion is dominant and are hence apt to be quickly, geologically speak-

ing, worn away with all their included organic remains. Those deposits are thicker and stand a much better chance of preservation, which are poured by continent-draining rivers into the sea as a delta. The delta and flood plain of the Ganges and Indus rivers (Early Tertiary to present) and that forming the Mauch Chunk shales (Mississippian) of Pennsylvania are good examples. The seaward portion of these deposits, being more continuously under water, is best able to preserve the organic remains deposited in it; hence we find the Greenbrier formation, interfingering the Mauch Chunk shales in southwestern Pennsylvania, full of marine fossils. The landward portion is covered with water and its accompanying layer of sediment only during times of flood when the river overflows its banks; during the rest of the year the level of the ground water sinks to a greater and greater depth, gradually dissolving all soluble objects as it moves, while the air circulates freely through the upper water-free deposits, completing the oxidation of all organic remains there present. The decay of plants or animals is an oxidizing process due largely to the multiplication of bacteria. Hence in these more landward deposits an organism encounters many agencies of destruction, both chemical and organic, and stands little chance of preservation. Thus in the Mauch Chunk shales of Pennsylvania and in the Newark beds (an Upper Triassic alluvial fan and flood plain deposit) of Connecticut, New Jersey, etc., few fossils occur and these are principally footprints and plant impressions. In portions of the Wasatch and Bridger formations (Eocene flood plain deposits) of Utah and Wyoming more fossils occur, but they are much more abundant in the Florissant beds (a Miocene lake deposit) of Colorado.

One of the best regions for the preservation of fossils is in the ocean at some distance from the land but upon the continental shelf. Here, constantly covered by the water, the organic remains accumulate in the depositing lime or limey shale sediments. They frequently form widespread beds of shells (coquina). Such bedded reefs are abundant on all continents

and in all ages. Such regions are favorable likewise for the formation of coral reefs, bryozoan reefs and algal reefs.

In short, the more completely air and circulating water are excluded from organic remains the better the chance for their preservation as fossils; and, accordingly, marine, lake, or marsh deposits are more favorable than those of a flood plain, alluvial fan, or playa, while clay or limestone are better mediums than sandstones or coarse ash deposits.

It is thus seen that the likelihood for the preservation of animals or plants varies with their habitat (Fig. 1). Inhabitants

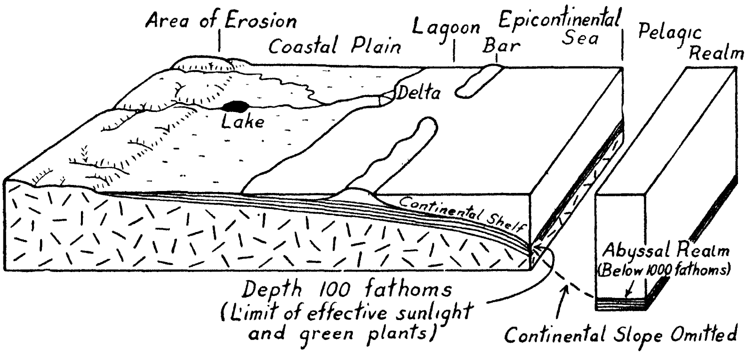


FIG. 1. — Diagram to illustrate various habitats of plants and animals and the consequent varying likelihood that an organism may be preserved as a fossil.

of mountainous regions where erosion is greater than deposition stand very poor chance for preservation in the fossil state; those living on low plains and in fresh water are more likely to be preserved; but it is the marine forms, especially those living upon the sea floor beyond the breakers but in water still comparatively shallow, that are most apt to persist. Here at their death the organic forms are quickly covered by the sediment which, brought in by the rivers or torn by the waves from the land, is widely distributed by the drift of the waters. Hence of all organic forms, marine invertebrates stand the best chance of preservation, for they are the most numerous of all animals

and they occupy those areas where oxidation is slow and where a prolonged sedimentation is apt to occur; these forms are, accordingly, the most important of all fossils for the correlation of strata. It is not strange, therefore, that many species of fossil insects are known each from but a single specimen, and that such a land form as Archæopteryx — the earliest known bird — is represented by only two specimens and a separate feather, all from the lithographic limestone quarries (Upper Jurassic) of Solenhofen, Bavaria. Species of fossil marine shells, on the other hand, are known by thousands of individuals.

3. Hard and hence preservable parts must be present in the organism (there are a few exceptions noted below).

To insure preservation it is usually necessary that the organism have some protective or supporting structure, such as the shell of a clam, the bones of a reptile, or the woody fiber of a tree, which upon the death of the animal or plant resists decay for a much longer time than do the softer portions. Usually the less fibrous plants and the softer parts of animals — epithelium, nerves, muscles, and even cartilage and horn — quickly suffer decay; and only the skeleton or the external covering, composed of chitin, silica, or of the carbonate or phosphate of calcium, is preserved. Thus multitudes of animals, such as most protozoöns, jelly-fish, sea anemones, many bryozoans and mollusks, most worms, the tunicates, most parasites, and the embryos of most animals, which lack such hard parts, are exceedingly rare or entirely wanting as fossils. Since the vast majority of the invertebrates living in the sea or fresh water are naked or provided with very fragile hard parts, it is only the bottom-living forms, which, in their heavy, protective hard parts, are usually preserved. Notwithstanding the rapid decay of all soft tissues these are occasionally preserved, as for example, by freezing in the bog-ice of Siberia, by carbonization (page 13), even by the taking up of lime phosphate on the part of the epidermal and muscular tissues, or by desiccation. Animals without hard parts at times also leave a record of

themselves, such as trails (like those due to the tentacles of a jelly-fish), internal molds (as the sand-fillings of the lobed pouches of the jelly-fish, Fig. 64), or as impressions of the entire jelly-fish, of leaves, etc.

Only rarely are plants protected by calcium carbonate or silica (page 10); usually their preservation is due to direct replacement, to the formation of external molds or to the process of carbonization (page 13).

Imperfection of the paleontologic record. — The vast majority of animal and plant remains that escape partial or complete disintegration and become preserved as fossils will probably remain forever unknown to man. The rock in which they are embedded may never be raised so that erosion along some stream course may expose the included fossils to view. Finally, it is only when a man with a trained eye and an interested mind happens to see such a weathered out fossil that it may become added to the paleontologic record of the earth. To these hazards of preservation must be added the consideration that upon every continent miles of fossil-bearing rocks have been eroded through the millions of years of earth history or have had their fossil contents destroyed through the metamorphism of the enclosing rock.

Williston has summed up the imperfection of the paleontologic record in his statement of the conviction that we can never hope to find even a single fossil of perhaps the majority, which must have numbered many millions, of the species of plants and animals that have lived upon the earth.

Processes of fossilization: ***1. Fossils unaltered*** (***original***).— All organic remains last longer in a region of almost continuous dry or cold than in one which is moister and warmer. In very cold, or very dry, regions, even the softer portions may remain unchanged for a long time, preserving to future ages the entire animal. Thus, examples of the ancient elephant — the mammoth — entombed in the ice and frozen earth of Siberia since the Pleistocene, are so well preserved that dogs and wolves will eat their flesh. Likewise, remains of the cliff dwellers in

Arizona and New Mexico, such as clothing, food, and human bodies, have been preserved in the dry air of that plateau region for at least many hundreds of years. Many Tertiary insects persist in their entirety, except for complete desiccation, without a trace of mineral infiltration, inclosed in amber; upon this ancient resin as it was exuding from the pine trees, insects settled, and, being held fast by the sticky substance, were finally entirely inclosed. These trees and their resin were buried in the sediment beneath the waters of seas or large lakes, thus preserving these ancient insects in all their perfection of form and brilliant coloring. (Resin, soluble in ether, alcohol, etc., but insoluble in water, is exuded by pine trees, firs, etc., and gradually hardens in air. Rosin, used on violin bows, is the commonest type. Resins are used in varnishes. Gum, soluble in water but insoluble in alcohol, is the product of many plants, as the cherry tree. It is much used in making vegetable adhesives.)

Usually, however, only the hard parts of organisms are preserved, and but few of these are found in an unaltered state in pre-Cretaceous rocks; it is principally in the Cenozoic rocks that they thus occur. The unaltered bone is more or less spongy in appearance, somewhat resembling volcanic pumice or slag; most of the cavities of the bone, however, are canals, continuous and anastomosing and do not end blindly as do those in slag. These Haversian canals, filled during the life of the animal with arteries, veins, and nerves, are much larger and more numerous in the interior of the bone than in the more compact and consequently harder outer portion. Non-petrified shells of Cenozoic or older age, besides having lost much or all of their original color, are usually also somewhat chalky in appearance because of the loss of the fleshy material within the living shell. (The abundance of this spongy animal matter may be demonstrated by an experiment. If a recent shell be placed in a dilute acid which is changed frequently, in two or three days the calcium carbonate will be dissolved away but the shape of the shell will still be retained by the animal matter which formerly penetrated it.) Thus shells from the Sankaty beds (Pleistocene) of Nantucket,

Massachusetts, differ from the recent shells only in their porosity and in having lost much of their color.

2. Fossils altered (*petrifactions*).—Whenever organic remains are inclosed in sediment to which the air has free access, their disintegration is rapid and complete (page 2); but if the deposits become very thick before they are raised from the water, free air will be largely excluded and destruction of the fossils will be principally due to the percolation of the water through the strata

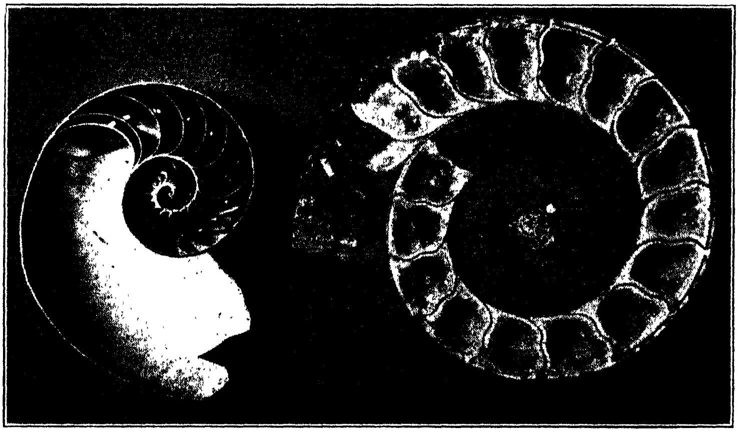


FIG. 2. — Longitudinal section through two cephalopod shells (× $\frac{1}{5}$). At the left the shell of the living Nautilus, with empty chambers. At the right the Jurassic Parkinsonia, with some chambers filled with mud while it was being buried, and the others partially or completely filled much later by calcite carried by infiltrating waters. The latter fillings are beautiful examples of geodes.

from higher to lower levels. That heat is not necessary in the solution of shells is seen in many deposits of glacial age. For example, the drumlins in and to the south of Boston Harbor, which have remained surface deposits from the time of their formation, contain no shells in the upper oxidized portion, but below that level they are quite fossiliferous. Here it could only be the cool acids, those from the decay of plants and the very dilute carbonic acid from rain drops, that caused the gradual solution of the shells.

Silicification, calcification, pyritization. — If the percolating water is a supersaturated solution of some mineral substance, such as silica, lime, or iron, the first step in the petrifaction of the fossil will be the *filling of all its existing cavities* with this substance (Fig. 2). In such a case the original chemical composition of the shell, bone, or wood will remain, but with the many

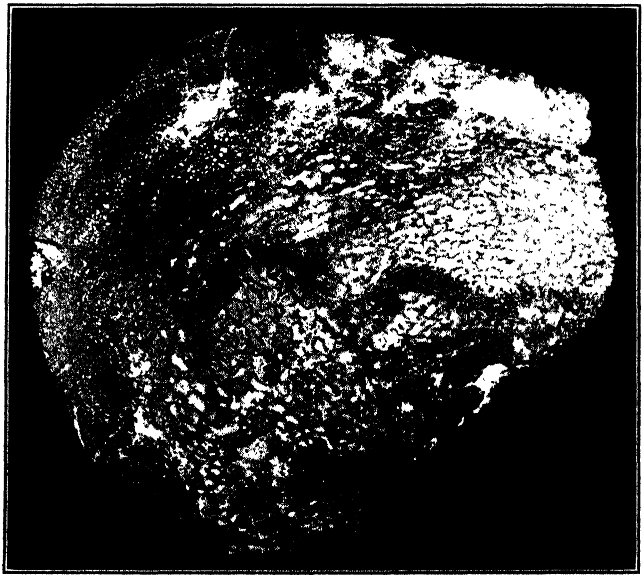


FIG. 3. — Polished section of an almost complete thigh bone of Brontosaurus, from the Morrison formation (Upper Jurassic and Lower Cretaceous) of Wyoming. This shows an early stage in fossilization, the filling of the Haversian canals with silica (× ⅜).

openings filled with the foreign mineral. This is the condition of many of the dinosaur and other vertebrate bones of the Mesozoic (Figs. 3, 4). *Molecular replacement.* — Often, however, the petrifaction, or making into stone, is a process of solution and deposition taking place *pari passu*, and due to the waters being undersaturated with the chemical substances of which the fossil is composed, but oversaturated with some other substance.

Such a replacement is at times very perfect. The probable process is that as a molecule of the original structure is removed, a molecule of the depositing substance takes its place; in this case the finer structure, such as the fiber in wood, or the pores and lamellæ in shells, is perfectly preserved. Such preservation of the finer details of structure is seen in many of the sections of the trunks of petrified (silicified) trees from the fossil forests

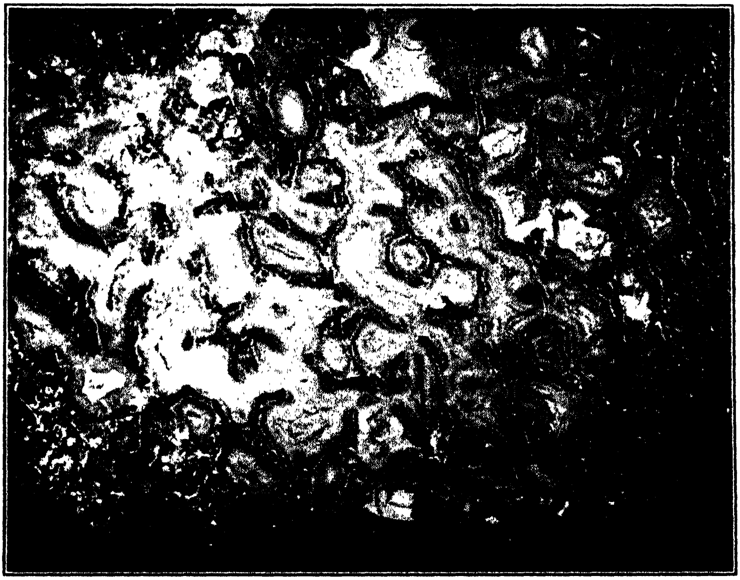


FIG. 4. — An enlargement of a small portion of the preceding. The darker portions are bone, the lighter are silica.

of the Yellowstone National Park (Fig. 5), from Adamana, Arizona, and from many other regions. In the case of the silicification of plants, the wood may act as a sponge, capillary attraction drawing up the colloidal silica, which, coming in contact with the carbon dioxide formed by the decay of some of the wood, is deposited, forming a solid. The colloidal silica later changes into the cryptocrystalline chalcedony. This often encloses various metallic oxides, such as iron. copper, and

manganese, giving various colors to the petrified trees (Fig. 5). The source of this silica is usually the inclosing strata, at times aided by uprising thermal waters. Silica is soluble in pure water, but especially in waters containing carbonates of the alkalies (Na, K), derived from leakage through the soil.

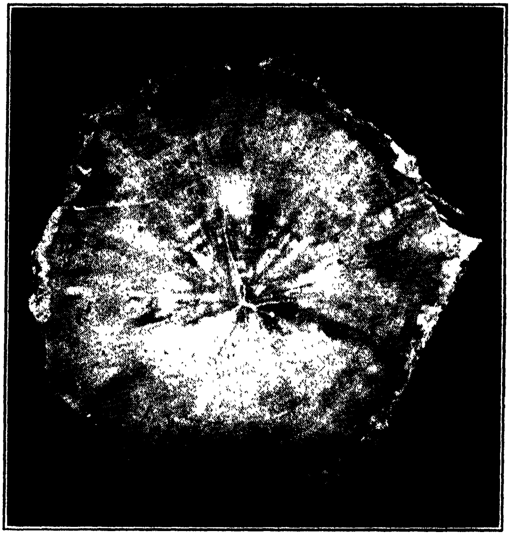


FIG. 5. — Polished section of a silicified tree (Araucaryoxylon) from Adamana, Arizona (× ⅓). The various dark spots in the photograph are shades of red due to iron.

Precipitation of silica may also occur through the agency of the carbon dioxide evolved by a living organism, such as the diatom, which thus manufactures its siliceous skeleton. The siliceous skeleton of organisms is composed of hydrous silica and is subject to dehydration into chalcedony, or to a later crystallization into quartz. Hence deposits of the minute diatom skeletons (about 40 million to the cubic inch), known as tripolite, are rarely older than the Tertiary, since the older deposits have probably been dissolved and redeposited as chert.

Similar replacement by silica occurs very frequently at the surface of a rock; probably the majority of silicified shells are thus formed.

With *iron*, replacement also takes place in the presence of organic substances; percolating waters rich in iron and sulfur will be precipitated upon coming into contact with these, causing

the formation of marcasite or of iron pyrites (FeS_2) (Figs. 6, 7). Molecular replacement is most common with silica, lime, and iron.

It is thus seen that the present composition of a fossil is no indication of its original composition, for there may be iron or siliceous replacements (pseudomorphs) of calcareous shells, iron pseudomorphs after chitinous skeletons and plants, and even, as in some sponges, calcareous pseudomorphs after siliceous skeletons. The determination of the original composition depends, in such cases, upon comparison of the form of the organism with the nearest living representatives.

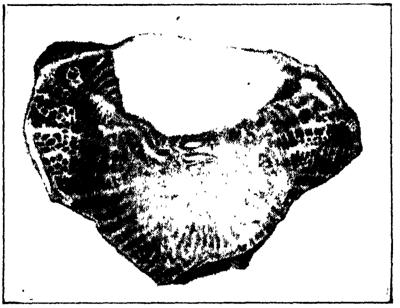


FIG. 6. — *Iron replacing lime* in the Devonian coral, *Heliophyllum halli* E & H, from New York. Natural size. The iron forms the ramifying white lines upon each side; this largely follows the septa, but it branches from these in all directions.

Carbonization. — If leaves fall into water, they sooner or later sink to the bottom, where they may be noted along the tree-lined margin of any lake or quiet stream; in such a place comparatively little free oxygen can reach them. Decay accordingly is very slow and usually but partial, leaving a residue of carbon; this, made fine by the motion of the water, gives the black color so characteristic of such bottoms. The form of the leaves under these conditions is, accordingly, not preserved, but their presence is indicated by the black color still persisting after these ancient lake and river margins have hardened into rock. Other leaves, though suffering a similar concentration of carbon, fall in a situation that insures their more rapid burial by the mud brought in by the rivers; they are accordingly preserved as carbonized films, showing all their original veining. This same process would occur in the case of any other form of vegetation or even of animals (Graptozoa, Crustacea, fish, etc.), if they were buried beyond the reach of scavengers.

The process of carbonization is essentially the giving off of marsh gas (CH_4), water (H_2O), and carbon dioxide (CO_2); the last cannot be developed to the exhaustion of the carbon, since, compared with air, little free oxygen exists in standing water.

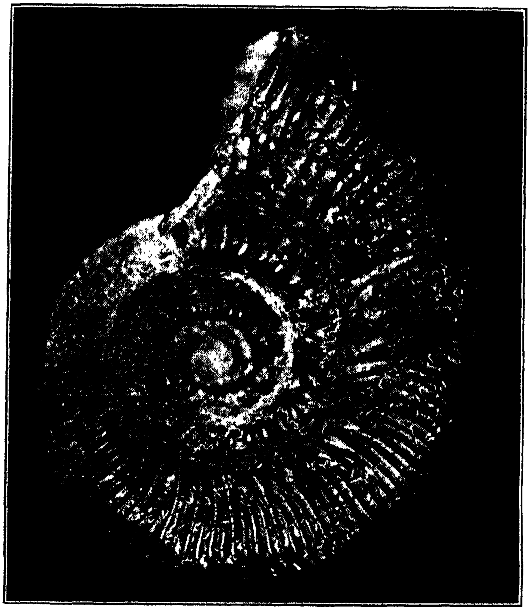


FIG. 7. — An ammonite shell (× 2), originally of lime, entirely replaced by pyrite.

Thus wood ($6\ C_6H_{10}O_5$) under such conditions would eventually yield an anthracite coal ($C_{24}H_8O$).

Good examples of carbonized plant fossils occur in the roof shales of coal mines (Fig. 8). Remains of animals similarly preserved are likewise abundant; well-known examples are Graptozoa (graptolites) in the Utica shales (Ordovician) of eastern New York, and fish in the Newark beds (upper Triassic) of New Jersey and Massachusetts.

Objects indicating the former presence of organisms. — *Molds.* — When a leaf falls upon soft mud, it will impress

there its form and surface markings; but the sun may quickly curl its edges so that it will be blown away by the wind. If this impression or mold be covered by sediment, the imprint is preserved without the leaf itself being inclosed. The mold is thus shaped into the form and surface character of the original. If a shell, such as a clam or snail, be covered with sediment, it will impress its external ornamentation upon the surrounding material (Fig. 9, *B*). The motion of the water before the shell is fully covered will usually completely fill its interior with sediment; upon this filling is impressed the shell's internal ornamentation (Fig. 9, *D*). The external and internal molds have thus the exact form and surface characters of the exterior and interior of the shell. (Good examples of such molds may easily be made by taking a complete clam or ark shell, first dipping it in water, and then filling and surrounding it with plaster of paris moistened to a plastic state, Fig. 9.) The internal mold, *i.e.*, the filling of the complete shell, is often spoken of as the cast of the soft parts of the animal; just as the inorganic material which takes the place of the brain in a fossil animal is called the brain cast. In other words, a cast replaces something; it is material taking the place



FIG. 8. — An example of carbonization. Part of a frond of the seed-fern Pecopteris ($\times \frac{2}{5}$) abundant in the forests of the coal swamps in the Pennsylvanian of eastern North America.

of the original, while a mold is the imprint which the original makes.

If the waters percolating through the earth's strata are rich in some solvent, as carbonic acid, and poor in lime, they will dissolve the calcareous shells from between their external and

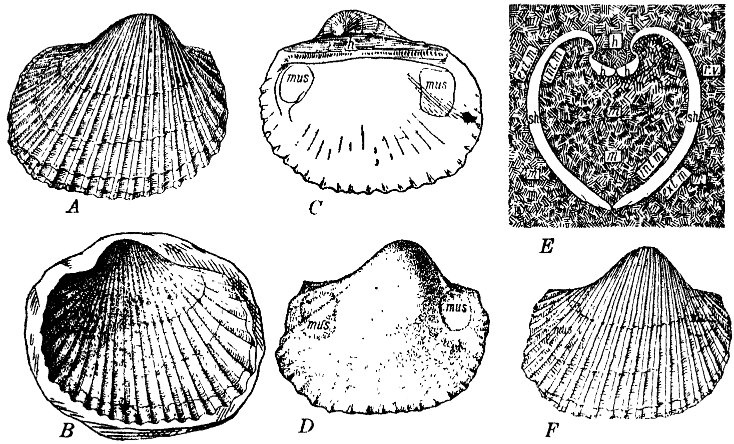


FIG. 9. — Diagram to explain *molds*, external and internal, and casts (× ½). The shell is the common ark, *Arca transversa* from Long Island Sound. *A*, external surface of right valve; *B*, the concave external mold of same valve; *C*, interior view of right valve; *D*, internal mold of same valve; *E*, section through entire shell from hinge-line (*h*) forward, the shell being embedded in and filled with sediment (*m*); *F*, external ornamentation impressed upon the internal ornamentation through the settling of the sediment after the chemical removal of the shell (as from *E*) by water percolating through the strata. *ext. m.*, external mold; *h*, hinge-line; *int. m.*, internal mold; *m*, matrix, or sediment; *mus.*, muscle scars; *r. v.*, right valve; *sh.*, shell (or, if shell is removed and this cavity is filled by some foreign substance, this substance is termed a *cast* of the valve, since it is formed between molds).

internal molds, and carry them away as a solution of bicarbonate of lime, leaving hollows where the shells were. In such a case one of three things happens: (1) there remains an open cavity, as in much of the Devonian (Oriskany) sandstone (Fig. 10) of eastern New York, Pennsylvania, and New Jersey; (2) through the settling of the strata the external mold comes into contact

with the internal (Fig. 9, *F*), and the external ornamentation thus becomes impressed upon the interior markings, as in many brachiopod and pelecypod shells from the Paleozoic; or (3) a petrifaction will be formed; *i.e.*, through a change in the direction of flow due to a differential upheaval of the region, or some other cause, the percolating waters become supersaturated with, for example, silica, lime, or iron; these hollows will then be

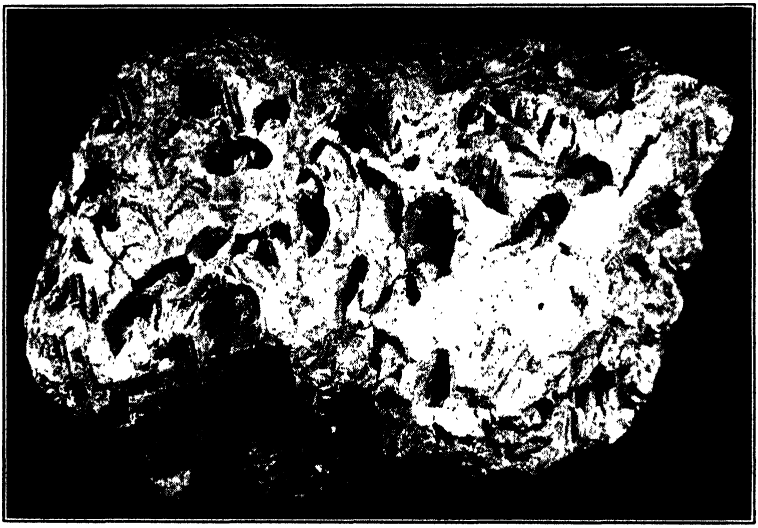


FIG. 10. — The early Devonian fossils (brachiopods) were carried away by percolating waters, leaving cavities which are surrounded by external molds.

filled and the foreign mineral will be shaped by the molds already formed into a *cast* (Fig. 9, *E*). Such a cast will bear an exact surface likeness to the original shell, but will lack entirely its internal structure. It is in such formation of a cast that the external and internal molds perform the true function of molds as usually defined, since they are thus " that in which something is molded or formed." (Iron fossils must usually be covered with a thin coating of melted paraffin to prevent a rapid rusting — oxidation and hydration — upon exposure to the air.)

When the shell has been removed, leaving an open cavity, the shape and ornamentation of the original shell may be obtained by pressing into it dental wax softened by heating in hot water, forming thus an artificial cast. Soft plaster of paris may likewise be used. If, however, the cavity is partially closed, the mold must be destroyed in extracting the cast. This method of restoring the form of the organism must frequently be used, since plants and animals are often coated with stone while the organic structure is still perfectly retained; upon the decay of the inclosed organism, which occurs rather quickly, there is left a perfect external mold. In the ancient ash-covered town of Pompeii the use of plaster of paris has enabled the workmen to preserve the external form of several men and dogs buried by the fragmental material which fell during the Mt. Vesuvius eruption of 79 A.D.

When birds or other animals searching for food walk over the mud flats of a river or sea, impressions of their feet are left as *tracks*, which, when covered with sediment, may be preserved as fossils. Examples of such are the reptile tracks in the Upper Triassic shaly sandstones of the Connecticut Valley (Fig. 11) and the tracks of the Mississippian amphibian, *Paleosauropus primævus,* in the Mauch Chunk red shales of Pennsylvania.

Similar to the preservation of tracks is that of *trails*, though many of these are made on the soft sediment beneath the surface of the water. Trails are the irregular markings of animals, such as those due to the crawling of a worm or snail, the dragging tentacles of a jelly-fish, the impressions of the fins of fish or the markings left by the movements of crustaceans or sea urchins.

When a worm *burrows* and eats its way through rather compact earth the hole remains for some time and finer material may later be washed into it; when it burrows its way through very moist sediment, as at the seashore, the finer material is usually carried into the cavity immediately behind it by the water oozing in from the sides. In both of these cases the resultant is a tube of finer material surrounded by coarser; as, for example, Scolithus from the upper Cambrian sandstones of the Appa-

lachian region (Fig. 79). Burrows are likewise formed in rocks on exposed coasts by sea urchins, in rocks and wood by different species of pelecypods (Lithodomus, Teredo, etc.), in soft earth by mammals. All of these burrows are capable of preservation as fossils under favorable conditions.

Coprolites. — The contents of the intestine and the excrement of many ancient animals, especially of fish and reptiles,

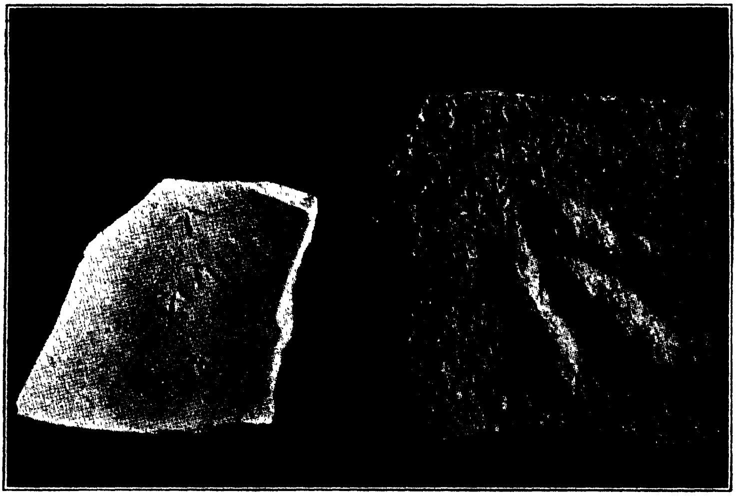


FIG. 11. — Footprints. At the left are tracks of a modern bird in the mud of the Bay of Fundy. At the right are tracks (in reverse) of a dinosaur in the hardened Triassic muds of the Connecticut River Valley. (From H. W. Shimer's *Introduction to Earth History*, courtesy of Ginn and Co.)

are often preserved and such fossils have received the name of coprolites. These are usually nodular or contorted in appearance and phosphatic in composition. They often contain such indigestible remnants of the animal's food as portions of scales, bones, teeth, or shells. Recent deposits are known as guano and are largely due to the excrement of sea birds and of such marine mammals as seals.

Fossil objects due to inorganic agencies. — Many objects due to inorganic agencies are often called fossils. It is in

accordance with general usage, however, to reserve this name for those objects having some relation to an organism, but the word fossil may be conveniently used as an adjective before objects due to inorganic agencies, such as ripple marks, to show that they have been preserved in the earth's strata. On the marginal flats of an ocean may be formed and preserved marks of ripples, cracks in the mud due to drying, imprints of rain drops, flows of mud due to an excess of water, and the marks showing the upper limit of the waves. But it is especially upon the mud flats of an aggrading stream or of temporary lakes, especially in the drier regions of the country, that very many and perfect ripple marks, mud cracks, and rain-drop imprints are formed and may persist. Such are the very regions where organic remains stand very slight chance of preservation, for the periodic removal of the water causes the rapid oxidation of all lifeless organic matter, so that the principal fossils present in such strata are tracks, trails, and burrows.

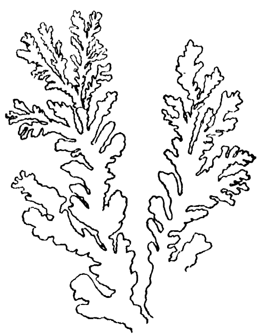


FIG. 12. — Dendrite (× 15), a branching incrustation, usually of manganese oxide. It reveals its inorganic nature in the complete irregularity of its branching. Drawn from the fractured surface of a Pleistocene shell.

Pseudo-fossils. — The slipping and twisting of strata likewise produce forms that at times closely resemble organic remains. These pseudo-fossils are especially noticeable in metamorphic rocks. The slipping of one rock face against another along a fault plane produces slickensides which are often closely similar to the Carboniferous plant, Cordaites, or at times to Calamites. The surface of a fossil, however, will be parallel to the lamina, whether it is the organism itself or its external mold, since it could normally have been deposited only in a position parallel with the bedding of the strata, whereas the slickenside will be seen usually to cross successive laminæ or even beds. Sometimes fractures, especially in dense, fine-grained rocks,

resemble the external molds of pelecypods or other bivalve shells. An inorganic form very often mistaken for true organic remains is the *dendrite* (Figs. 12, 13). Dendrites are crystalline structures of branching form resulting from a preponderance of growth along the direction of the crystalline axes. They crystallize from a colloidal solution. These branching incrustations, formed usually of manganese oxide, are common, either inclosed, as in the moss agate, or merely as surface markings. They look much like a piece of moss or fern, but there is no regularity in their method of branching, whereas an organism always exhibits a regularity, a symmetry.



FIG. 13. — Photograph of dendrite on Jurassic limestone from Solenhofen, Bavaria. Natural size.

Classification of fossils. — *A fossil is the remains of a plant or animal, or the record of its presence, preserved in the rocks of the earth.*

The word is derived from the Latin *fodere*, to dig, and hence has associated with it the thought of something dug up, for in most cases the preservation of a form depends upon its burial. Some geologists restrict the term fossil so as to include evidences of life preserved in rocks deposited up to the close of the Pleistocene only. According to this definition[1] all post-Pleistocene remains are spoken of as recent, not fossil. By extension of the term, fossil is at times used as an adjective for certain inorganic structures.

Fossilization is the sum of the phenomena by which the remains of animals or plants, or the evidences of their presence are preserved in the earth's strata.

Fossils may be divided according to the above definition into,

I. Fossilized remains of organisms

II. Objects indicating the former presence of organisms.

Sometimes these fossils preserve their original composition as when first buried, that is, they are *unaltered.* At other times they become more or less completely *altered* by infiltration of minerals from the surrounding rocks, or the more volatile parts are gradually given off, leaving a residue composed very largely of carbon. It is to such " altered " fossils only that the term petrifaction, *i.e.*, " turned to stone," should be applied.

I. FOSSILIZED REMAINS OF ORGANISMS.

A. **Unaltered** (*i.e.*, original).

1. Originally soft portions of the animal preserved. Examples: insects in amber; mammoths in frozen earth of Siberia.

2. Only hard parts preserved. Examples: many Cenozoic shells, bones, teeth, horns.

B. **Altered** (*i.e.*, petrifactions). These are due to (*a*) the filling of the cavities within the substance of the shell, bone, etc., which during life were occupied by soft tissue (p. 10); this is partial petrifaction; (*b*) molecular replacement (p. 10); (*c*) formation of casts (p. 17); (*d*) the chemical reduction of the hard parts in which hydrocarbons are present (Carbonization, p. 13).

Petrifactions are also divided into four main divisions according to the material petrifying them. Although silica, lime carbonate, and iron pyrites are the most common replacing minerals, 30 to 40 others replace more rarely.

1. *Through silicification.* — Varying from the merely partial filling of cavities within the substance of the fossils (even if originally composed of silica) to entire replacement with silica. Examples: Shells, plants.

2. *Through calcification.* — Varying from the merely partial filling of cavities within the substance of the fossils (even if originally composed of calcium carbonate) to entire replacement with calcium carbonate. Examples: Most fossil corals, brachiopods, echinoderms, mollusks.

3. *Through pyritization.* — Varying from the merely partial filling of cavities within the substance of the fossils, to entire replacement with pyrite or marcasite. Examples: Shells, crustaceans, plants.

4. *Through carbonization.* — Animal or vegetable tissue decomposed under water, resulting in a giving off of comparatively more hydrogen and oxygen than carbon, with a resultant concentration of carbon. Examples: Fish, graptolites, plants.

II. OBJECTS INDICATING THE FORMER PRESENCE OF ORGANISMS.

A. **Molds, external and internal.**

1. Imprints of shells, feathers, tree trunks, entire animal.
2. Tracks of amphibians, reptiles, birds, etc.
3. Trails of worms, crustaceans, etc.
4. Burrows of worms, echinoids, mammals, etc.

B. **Coprolites.**

C. **Artificial structures.** Examples: Birds' nests, early human implements.

III. INORGANIC AND PSEUDO-FOSSIL OBJECTS.

1. Fossil objects due to inorganic agencies. Examples, ripple marks, mud cracks, raindrop impressions.
2. Pseudo-fossils. Examples: slickensides, dendrites.

Restoration of fossils. — Since fossil organisms are built on the same general plan as living ones, a reconstruction of their appearance when living, like their identification and classification, is a matter of comparison. The broader and deeper one's knowledge of living species, the nearer the truth one's conclusions are apt to be. The relation between the soft, unpreservable portions of an animal, and the hard parts capable of preservation, is very close. The shell, for example, is such an

intimate part of the animal that an injury to it means a lessening of the vitality of the entire organism, while the loss of it means death (Fig. 14). It is, accordingly, incorrect to speak of the animal and its shell as though the shell were a house which the animal could leave at will. An invertebrate animal may thus be divided, for convenience of description, into body (the soft

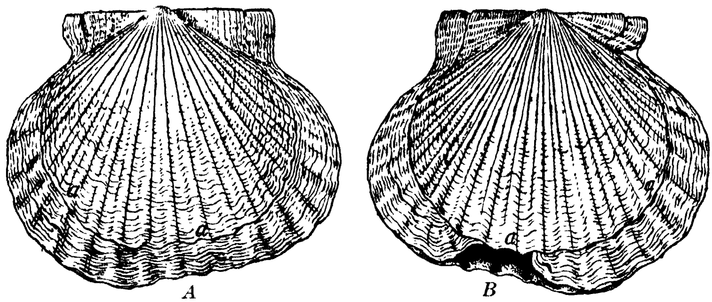


FIG. 14. — The intimate relationship which exists between the hard shell and the soft body of an animal is seen here in the scallop, *Pecten gibbus borealis*, from the New England coast. *A*, outer surface of left or upper valve; *B*, right valve, with the left showing slightly at the base. The mantle secreting the right valve (*B*) received an injury when the edge of the shell was the growth line *a-a'*; this injury lowered at once the vitality of the entire body, so that anterior growth of both mantles wholly ceased for a time, a fact recorded in the conspicuous growth line *a-a'*. Though the animal lived for some time after this injury it never regained its former vitality, as is shown in the development of such old-age characters as the obsolescence of the ribs and the irregularity of the growth lines. The mantle at *a* upon the right valve ceased growing entirely, but the opening thus made was partially filled by the inbending of the opposite valve. (Slightly reduced.)

parts) and shell; a vertebrate may be considered as flesh and skeleton.

In restoring a fossil to its living appearance, truthfulness of detail depends largely upon the fineness of the material in which it has been preserved. In very fine-grained shales and limestones impressions of the soft parts are often preserved to even minute details. Thus in making a restoration of the trilobite, Triarthrus, the Utica shale in New York State furnished not only

the legs, antennæ, and gills, but traces of the digestive tube as well (Fig. 155). The Lithographic limestone in Bavaria and the Oxford clays in England show by the preservation of arms, outline of body and ink sac that the Mesozoic belemnoids were very similar to the living squid, while in the shale of the Burgess formation of British Columbia, occur beautiful impressions of such soft-bodied animals as jelly-fish, worms (Fig. 15), and sea cucumbers. In trilobites there is usually preserved only the hard dorsal shield; in belemnoids only the small, internal

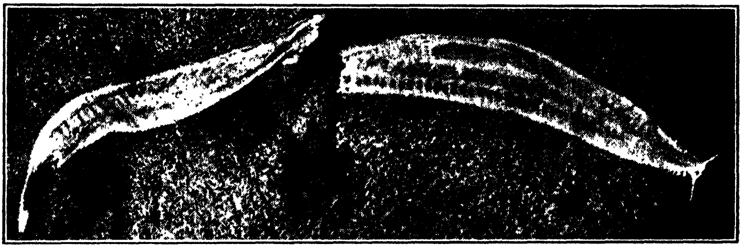


FIG. 15. — The gephyrean worm, *Pikaia gracilens* Walcott (× 2) from the Middle Cambrian (Burgess shale) of British Columbia. In these fine-grained shales are preserved the head, the anterior parapodia, segmentation of the body, and the outline of the digestive canal. (After Walcott.)

skeleton; in worms, teeth; and in sea cucumbers scattered calcareous plates.

In all vertebrate animals muscles are fastened to an internal skeleton by projections, roughened surfaces or depressions upon its surface; the larger such surface or projection, the larger the muscle attached to it. Hence from the bone alone the number and size of the muscles formerly attached to it can be estimated. Since muscles and bones make up the main bulk of the animal, a restoration to living proportions is possible. The shape of the teeth tells the character of its diet, which in turn reveals the size of the digestive organs. The superficial covering, however, is often a matter of conjecture. In fish the covering of scales is usually preserved; in amphibians mucus gland impressions often show upon the surface of the bones, thus indicating a soft, slimy

skin for the animal; in reptiles the preservation of scales or bony denticles or their impressions indicates the character of the external covering (Fig. 16). When, however, as often happens, nothing of the sort is preserved, the restoration must be based upon comparison with other fossils and with living forms; especially suggestive are the young of nearly related living species. Studies in evolution have shown that each individual in its development from the egg to maturity passes through stages which are similar in general to its successive adult ancestors from earliest geologic ages to the present. Hence a stage in the youth of a living animal would be suggestive of related extinct forms. This principle, however, must be applied with the greatest caution. The adult elephant and rhinoceros are almost hairless, while the young have much hair; that this may be reminiscent of the ancestral forms is suggested by the Pleistocene hairy mammoths preserved in the Siberian ice fields. The coloration of the young likewise is difficult of explanation unless it be taken as representing that of its adult forbears. The young Malayan tapir is longitudinally banded, the adult loses these bands; the young wild swine are longitudinally banded, the adults are not; the young lion is spotted, the adult is of uniform coloration.

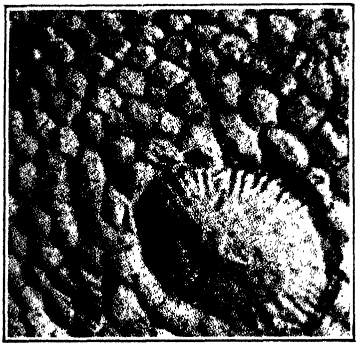


FIG. 16. — Natural mold of the surface markings of the dinosaur, *Stephanosaurus marginatus* Lambe, from the Cretaceous of Alberta. These markings are from the side of the body, where the yielding mud receiving the impression of the skin of the reptile upon its burial, has preserved them intact though the skin itself has long since disappeared. (From Lambe.)

Color of fossils. — Recent organic calcium carbonate, such as occurs in shells and corals, is white, except for the occasional presence of a pigment or epidermis; Tertiary shells are darker, while those from the Paleozoic are, as a rule, darkest. Like-

wise, whereas many recent shells are lined with mother-of-pearl, very little is found in pre-Mesozoic shells. These changes are due to one or more of several causes. The chalky aragonite becomes changed to the darker calcite. As the pores and interstices become filled with some foreign substance light is excluded and a darker color results. If the inclosing sediment is dark in color, the fossil will be stained by it more and more deeply according to the length of time inclosed. A secondary replacement by calcium carbonate may likewise be accompanied by foreign impurities, such as carbon or iron sulfide, and thus produce a darker color. Hence the older the fossil, the greater is the probability of the shell being dark. This generalization holds true too for vertebrate and arthropod remains, though in these cases the increasing dark color is mostly due to carbonization.

The process of fossilization likewise rapidly destroys the epidermis and the pigment present on many shells. Very little pigment remains in pre-Cretaceous shells. Where shells are light colored and originally had color bands, such may be at times preserved in fossils as dark bands.

Distortion of fossils. — In the bending, twisting, slipping, and crushing of portions of strata that are usually consequent upon the upheaval of great thicknesses of sediment from a region of deposition into a region of erosion, more or less distortion of the included fossils must occur. At times, merely the great weight of the overlying sediment causes distortion. It is necessary, accordingly, to critically examine the fossil and, if possible, compare it with others of the same species to fully determine its original shape.

Elements in living organisms. — In both animals and plants carbon, oxygen and hydrogen, nitrogen, phosphorus, sulfur, potassium, iron, sodium, and chlorine are always present. Of these, the first four elements are the most abundant. In addition to the above, the following are at times found in both plants and animals: magnesium, calcium, silicon, iodine, manganese, fluorine, copper, and aluminum. Of still more rare occurrence

are arsenic, barium, boron, cobalt, lead, lithium, nickel, radium strontium, and zinc.

In a pure state the cellulose of plants is composed of carbon, oxygen, and hydrogen, but in the form of wood fiber it contains in addition varying percentages of potassium, sodium, calcium, magnesium, iron, phosphorus, sulphur, silicon, and chlorine, also usually traces of copper. Some of these elements may be present simply through mechanical storage and play no active rôle in the physiology of the plant. Potassium is abundant in seaweeds, especially in the kelps. Calcium appears in the compounds lime carbonate and lime phosphate. Magnesium is often associated in rather large percentages with lime carbonate in some marine lime-secreting algæ (nullipores), echinoderms, corals, calcareous sponges, and foraminifers; this is a first step in the formation of dolomite, the double carbonate of calcium and magnesium. In vertebrates and many invertebrates iron is essential in the hemoglobin of the blood as an oxygen carrier. In many of the invertebrates (some mollusks, crustaceans, and insects) copper is the essential element in the hemocyanin of the blood as an oxygen carrier; in these animals the final source of these elements is probably the plants. Chlorine is present in many plants and in all animals; in the latter it is an essential element in the gastric juice, the principal food-dissolving acid from amœba to man. Silica is found in all plants and in many animals.

Composition of the hard parts of organisms. — The composition of the hard parts varies considerably in different organisms and consequently causes a variation in the preservation of the different forms as fossils. For example, percolating waters dissolve aragonite with great ease, but have little effect upon chitin.

The following list contains the essential mineral composition of the hard parts of the more important animal and plant classes:

Animals. — 1. *Lime carbonate:* Foraminifera (most); sponges (some); Hydrozoa (some); corals (most); Molluscoidea (most); mollusks (most); Echinodermata (all).

(*a*) Calcite ($CaCO_3$): Foraminifera (vitreo-calcareous forms, such as Globigerina); corals (many); sponges (Calcarea); Bryozoa (most); brachiopods (all except the phosphatic ones); worms (Serpula, etc.); Crustacea (calcareous part of skeleton); Pelecypoda (many entirely of calcite, as Pecten, Ostrea; many with only outer layer of calcite and inner of aragonite, as Mytilus, Unio); Gastropoda (few, as Scalaria; some, as Patella and Littorina, have only outer layer of calcite); Cephalopoda (few, as Argonauta and Belemnites); Echinodermata (all); hens' eggs.

(*b*) Aragonite ($CaCO_3$): Foraminifera (probably most porcellanous forms, as Peneroplis); corals (Madreporaria); most scaphopods, pelecypods, gastropods, and cephalopods.

Calcite and aragonite have the same composition ($CaCO_3$) but crystallize in different systems. Aragonite crystallizes in the orthorhombic system; in shells it usually has a chalky, opaque appearance and is compact throughout. Calcite crystallizes in the hexagonal system; in shells it is usually translucent, with a compact surface but porous interior. In carbonic acid it dissolves more slowly than aragonite and hence when subject to percolating waters persists longer. In *Mytilus edulis*, the outer layer of the shell is of calcite, the inner of aragonite; many of these shells from the Pleistocene have the calcite preserved but the aragonite dissolved away. Hence it is seen why shells of brachiopods are better preserved fossils than those of mollusks.

Calcite may be distinguished from aragonite by the following simple method: powder the substance and boil one minute in dilute cobalt nitrate; if it is aragonite the precipitate will be of a pink or lilac color; calcite, even with longer boiling, will remain white (or at times somewhat yellowish from the presence of some organic substance).

2. *Silica.* — Radiolaria (most); sponges (Silicispongiæ; this order contains most of the fossil and many of the recent sponges).

(Silica (SiO_2), in the form of quartz, is one of the most stable

of minerals, but when secreted by an organism, it contains some water, is glassy and isotropic, *i.e.*, is penetrated by light and heat equally in every direction; in this condition it is dissolved with comparative ease by percolating waters containing alkali.)

3. *Chitin* ($C_{15}H_{26}N_2O_{10}$). — Foraminifera (few); sponges (Ceratospongiæ); Hydrozoa (most, Leptolinæ) and Graptozoa; corals (axis of sea-fan, etc.); arthropods. (The word chitin is here used in a general sense and does not imply a chemical and structural identity with the true chitin of the Arthropoda.) Chitin is resistant to both acids and alkalies.

4. *Lime phosphate.* — Brachiopods (a few, as Lingula, etc.); vertebrates (about 40 per cent of the ash of bones is phosphoric acid).

5. *Cellulose* ($C_6H_{10}O_5$). — Protozoa (a few); ascidians.

Plants. — 1. *Cellulose* ($C_6H_{10}O_5$). — All plants from the thallophytes up, with a few exceptions.

2. *Silica* (SiO_2). — More or less silica is present in the cell walls of all plants; it is especially abundant in diatoms, equisetes (horsetails), Carex, margins of grass blades, etc. In diatoms, the form of the plant is retained by it after the burning away of the organic matter.

3. *Lime carbonate* ($CaCO_3$). — This forms a thick white coating on many algæ, as *Corallina officinalis* (a red alga), Lithothamnion (a red alga), and Halimeda (a green alga); the last two are most important in the building up of coral reefs; the freshwater alga, Chara, is an important agent in the formation of marl.

Order of preservation of organic remains. — The preservability of organic remains depends upon a great variety of factors. Among these and applying to both land and water dwellers, are the abundance of scavengers, rapidity of burial, acids and alkalies present in the waters percolating through the strata which inclose the remains. In the case of land dwellers, the determining conditions include the humidity, the rainfall, the daily and yearly changes in temperature. In general, however, those

remains which have the best chance of being preserved are, in order of likelihood the following:

Chitin	Calcite
Teeth	Tendons
Cellulose	Cartilage
Resin	Aragonite
Calcium phosphate	Gum
Silica	Muscles

Nerves and blood vessels

Collecting fossils. — Fossils in crystalline limestone often weather out in high relief. This is usually due to the larger crystals of the fossils which are naturally less soluble. With the continued weathering away of the limestone these will become entirely silicified and will lie in the residual clays as ideal specimens. Weathering out of the entire compact fossil is also characteristic of shales, shaly limestones, and of marls, consolidated or unconsolidated. Hence excellent places for collecting fossils are along weathered rock surfaces, water courses leading from such rocks, or even in plowed fields, especially immediately after a rain.

Naming of organisms. — In early times, only variable common names or a single technical name was applied to a species of animal or plant; more often the name was long and descriptive. This procedure was first changed by the great Swedish naturalist, Linnæus (or Linné), who introduced the binomial, or two-name, method, a combination of a generic and a specific name for each different kind of plant and animal. His great work, *Systema Naturæ*, was published in 1735; this was in Latin, the scientific language of Europe at that time, hence all his technical names have Latin or Greek endings. This use of Latin and Greek was found so satisfactory, since the same names could be used by all nationalities and languages, that it now governs the naming of organisms the world over. As a result the technical name of an organism, fossil or living,

is the same whether used in English, German, Russian, or Japanese works.

Before Linnæus, the single technical name was often modified by a descriptive phrase; for example, one of the lady-bugs was called the Coccinella with the seven black spots; this Linnæus called *Coccinella septem-punctata.* The first of the two names is that of the genus and represents the broader relationship, the second is that of the species and includes all individuals which are almost exactly similar; this likewise follows the Latin order of names, the family name being placed first and the individual name last. The ancient Romans would not have said John Jones, but Jones John. It is the accepted practice to place after the binomial the name of the man who first used that particular species name, for example, *Coccinella septem-punctata Linné.* The generic name is at times the word by which the ancient Latins knew the plant or animal in question. Thus Pinus is the pine. Frequently the generic or specific names are descriptive; thus *Spirifer mucronatus* is the spire-bearing shell with mucronate ends. At times the names are given in honor of some person, as *Turritella mortoni*, after Doctor Morton.

What fossils tell us: *1. History of plants and animals.* — Fossils furnish not only the best evidence for the determination of the geographic history of the earth, the distribution of the seas and shores and mountains of the past; they supply as well a record, even though incomplete, of the animals and plants which peopled those continents and seas, from the beginning of life on earth over a billion years ago to the present.

2. Index fossils. — Every fossil is more or less an index to the age of the rock in which it occurs, for it is a relic of the life which inhabited the earth when that sediment which now forms the inclosing rock was being deposited. It was early observed that succeeding rocks contain different fossils, that as they were followed from the lower to the higher beds (*i.e.*, from the older to those more recent), the inclosed fossils changed. At present the succession of life in general upon the earth has

been determined, though more and more of its details are being discovered each year. It is known that these successive faunas and floras follow each other in the rocks the world over in approximately the same order.

It has been observed that each fossil is not of equal importance as an index to the age of a rock; some species occur in the strata of two periods, such as the brachiopod *Atrypa reticularis* in the Silurian and Devonian, while others are confined to a very small portion of one; that is, some have a great and others a limited vertical distribution or time endurance. Some are confined to the strata of a single locality, while others, such as the brachiopod *Productus semireticulatus*, occur in strata of similar age over the world; that is, some have a wide and others a limited horizontal distribution or geographic range. The best index fossils are those which combine a wide horizontal with a limited vertical distribution.

The study of Index Fossils is thus of great importance in determining the age of strata; they are indispensable guides in locating and following oil and coal-bearing beds, in making geological maps and sections, in working out faults, etc.

3. Migration and ancient geography. — Fossils tell us of the body of water in which the rocks inclosing them were laid down — whether shallow or deep, near to or far from land, open sea or inclosed basin. They tell us of changes in climate. They tell us of the presence of land barriers where now are none, of land bridges that formerly united lands now long separated. This knowledge of ancient geography that they give us is based upon the observed fact that species migrate. The larvæ of beach-dwelling creatures are carried by tide and waves along the edge of the sea and thus colonize new areas. Large bodies of water, however, few animals can cross, and hence, when the same species of the trilobite Trinucleus, for example, is found in Ordovician deposits of both Europe and America, we must assume a continuous beach line, a land bridge between the two continents at that time. Mammals migrate by walking and swimming, but they, too, are limited in range

by broad areas of water, high mountain ranges, etc. Thus the presence of the same species of elephant in the Pleistocene strata of both Europe and America indicates a land bridge at that time.

An example of the rate at which a species may migrate is found in the record of *Littorina littorea*, the common periwinkle. It is very abundant on the rocky shores of England. Since it does not occur in the fossil state, or in any of the prehistoric shell heaps in America, it is evident that it was introduced from Europe about the middle of the nineteenth century, for it was recorded from the Gulf of St. Lawrence in 1850. Thence it slowly spread southward along the coast, probably by the transport of its larvæ by the southward-flowing Greenland current. In 1870 a few were noted on the Maine coast; in 1872 it was found at Salem, in 1880 at New Haven, and in 1891 as far south as Delaware Bay. In each locality where observed it had become the most abundant gastropod within two or three years after its first appearance. On the New England coast it covers the rocks and seaweed between tide limits.

4. Climate. — The range of living plants and animals is largely limited by climatic conditions. Certain forms are associated with cold climates, others with swamps, others with dry deserts. It follows that fossil plants and to a less degree extinct animals can reveal much about the climatic conditions under which they lived, whether moist or dry, cold or warm, since the rock in which they are found is a hardened section of the ocean or river bed, swamp, or desert in which they lived.

5. Evolution. — Evidences for the theory of organic evolution are derived from four classes of observed scientific facts, those furnished namely by comparative anatomy, embryology, paleontology, and geographic distribution. The chief contribution is that of paleontology since it supplies definite lines of ancestry for living plants and animals.

Among birds, for example, the occurrence of the lizard-like Archeopteryx in the Jurassic, the more modern but still toothed birds in the Cretaceous, and the wholly modern toothless forms

in the Tertiary, shows the successive modifications that appeared in the ancestral line. This explains as ancestral stages such vestigial structures in embryos of living birds as teeth within the gums, claws upon the wings, and the numerous tail vertebræ.

In shells the evolutionary succession of individuals preserved as fossils in a succession of strata from lower to higher, that is, from earlier to later, suggests an ancestral line that can be checked in the successive stages of growth of an individual shell as measured by its growth lines from the beak outwards.

The science of paleontology. — The general study of living things is called biology. It includes botany, the science of plants, and zoölogy, the science of animals. Every science overlaps and shares part of the field of other sciences. Thus biology meets physics in the field of biophysics, it meets chemistry in biochemistry, and it meets geology in the field of paleontology. Paleontology is the science of the past life of the earth. It aids the botanist and zoölogist in gaining a knowledge of the ancestors of present-day plants and animals; it aids the geologist in determining the age and origin of the rocks in which the fossil remains occur.

Since present-day species of plants and animals are found to be related in varying degrees to other existing species, and since all of these in turn are shown to be related by descent to other species now extinct but present as fossils in strata laid down in more or less remote periods of the earth's history, it follows that all organic life, past and present, may be likened to a tree. All of this tree except the outermost twigs is buried in earth. It is these outermost or most recent twigs only which the zoölogist and botanist study. The paleontologist digs into the earth, revealing here a branch, there a portion of the trunk, but always also innumerable extinct twigs, representing prolific races which, having played their part upon the earth, have left no descendants to follow them.

Paleontology may be studied either as pure science or as applied science. To one interested in pure research, the dis-

covery of new facts about the past life of the earth and new interpretations of its evolution is a pursuit rewarding in itself. The worker in the field of applied science prefers to direct his effort towards the securing of scientific material which will in some way contribute to the discovery or exploitation of some geologic deposit desired by man.

Organic and inorganic matter. — Matter is either **organic** or **inorganic.** Organic matter is arranged in the form of a plant or animal body, and is so called because of it are made the various organs such as those for eating, breathing, and reproduction. In the lowest organisms the entire body forms but a single organ. When matter is not thus organized, as in air, earth, and water, it is called inorganic. Food in the shape of lifeless matter, including many inorganic substances and those organic substances in which all the organs have ceased functioning, is absorbed by functioning organisms, and in some manner, not understood, is transformed by them into living matter, that is, into protoplasm. For protoplasm is the only living matter, and through its activity is built up such supporting and protecting tissues as the cellulose of plants, the bone and shell of animals.

Protoplasm is the only living substance, and whether plant or animal, it has the following properties which distinguish it from lifeless matter: (1) Chemically it always contains proteids or albumins — complex compounds of carbon, hydrogen, oxygen, nitrogen, and sulfur. It contains, on the average, of carbon 52 per cent, of hydrogen 7 per cent, of nitrogen 16 per cent, of oxygen 23 per cent, and of sulfur 0.5–2.0 per cent, while iron is essential in its formation. The nucleoproteids, found in the cell nuclei, contain also a small amount of phosphorus. (The white of an egg is almost pure proteid plus much water.) (2) Physiologically it has the power of waste and repair, of growth and of reproduction.

Living organisms waste away by oxidation, a kind of internal combustion, but continually repair this waste by additions between the existing molecules. If this addition is greater than

that necessary for repair, growth occurs. Inorganic substances, on the other hand, such as crystals, grow solely by external addition. Living bodies likewise detach portions of themselves, which thus acquire independent existence and develop into the form of the parent.

Plants and animals distinguished. — Plants and animals differ fundamentally in their food; the former usually feed upon inorganic, and the latter upon organic matter. As a result of this, plants tend to a life of immobility, deriving their food from the soil, water, and air about them. They accomplish this through the agency of the sun's rays, which, working through the green coloring matter, chlorophyll, combine the unorganized elements into the complex products — proteids, carbohydrates, and fats. Animals, on the other hand, as a result of searching for their food, tend to a life of mobility, deriving their food from plants or other animals; hence chlorophyll is absent, and as a consequence of its absence starch is not manufactured and thus cellulose is likewise wanting. (All animals have freedom of movement at some period of their lives, even those sessile when adult, as the sponge, coral, and barnacle, which can move from place to place in their embryonic life.) These differences between plants and animals are, however, not absolute; some of the lower forms of each kingdom have properties which in their full development characterize the opposite kingdom. For example, among plants, fungi live upon organic matter, many algæ, as diatoms, spores of cryptogams, and the male sexual element of most plants have the power of locomotion; the dodder and most bacteria have no chlorophyll. Among animals the protozoön, Euglena, has chlorophyll, while cellulose is present in some Protozoa and is abundant even in the ascidians of the Chordata.

1. What fortuitous circumstances determine whether an organism becomes a fossil?
2. Name three kinds of deposits in which organisms may become buried and thus preserved.
3. Draw a diagram illustrating terrestrial and seashore deposits

and indicate the most favorable of all localities for the preservation of fossils.

4. Mention an example of a recent flood plain deposit in the United States; of a fossil flood plain. What kinds of fossils are we most apt to find there?

5. Give an example of a fossil lake deposit and the kind of fossils for which it is noted.

6. What is the best region for the preservation of marine fossils?

7. What significance has the expression, "imperfection of the paleontologic record"?

8. How may the entire bodies of animals at times be preserved?

9. What is amber? Loess?

10. Distinguish resin from gum.

11. How do you distinguish bone from slag?

12. Show that a lime shell contains much organic matter. Illustrate the destruction of shells by percolating waters.

13. What are the chief minerals concerned in fossilization?

14. What is the first step in the petrifaction of a fossil?

15. Define molecular replacement.

16. How does silica get in solution? Explain how it is precipitated in the silicification of wood.

17. What gives the various colors to petrified trees?

18. Explain the deposition of silica in the living diatom.

19. Explain the process of carbonization. Give examples.

20. Explain by diagram the formation of an external and an internal mold; of a cast.

21. Describe the process by which (*a*) a leaf is preserved and fossilized; (*b*) a clam shell; (*c*) a bone; (*d*) the burrow of a worm; (*e*) a jellyfish; (*f*) the track of a reptile; (*g*) the trail of a snail.

22. What are coprolites?

23. Name some "fossil" objects due to inorganic agencies.

24. Describe some pseudo-fossils.

25. Define and classify fossils.

26. What kinds of sediment are apt to best preserve the details of a plant or animal? Give examples.

27. Why is a shell affected by an injury to the mantle?

28. How may we form an opinion of the shape of a vertebrate animal merely by study of its skeleton?

29. How do we know the surface ornamentation of fossil fish, amphibians, reptiles, birds, mammals?

30. What changes in color does a shell undergo during fossilization?

31. Why are fossils at times distorted?

32. What elements are present in plants and animals?

33. Name the chemical elements essential to the life of plants and animals.

34. Discuss the composition of the hard parts of animals, with a few examples of each; of plants.

35. List the normal order of preservability of organic remains.

36. Where in the field would you look for fossils?

37. Who was Linné?

38. Explain and illustrate the binomial method of naming organisms.

39. What are index fossils? What constitutes a good index fossil? Of what economic importance are they?

40. How do animals migrate? Illustrate. What does a knowledge of migration tell us as to ancient geography?

41. What do fossils tell us about the climate of past ages?

42. What is the contribution of fossils to our knowledge of evolution? Illustrate.

43. Define Paleontology. Show its relation to other sciences. Distinguish between pure and applied Paleontology.

44. Distinguish between organic and inorganic matter.

45. What is protoplasm?

46. Give three differences between plants and animals.

GEOLOGIC TIME SCALE

Era		Period
Cenozoic	Quaternary	Holocene (Recent, or the present)
		Pleistocene (Glacial)
	Tertiary	Pliocene
		Miocene
		Oligocene
		Eocene
		Paleocene
Mesozoic		Upper Cretaceous
		Lower Cretaceous
		Jurassic
		Triassic
Paleozoic		Permian
		Pennsylvanian (Upper Carboniferous)
		Mississippian (Lower Carboniferous)
		Devonian
		Silurian
		Ordovician
		Cambrian
Proterozoic, Archeozoic		Pre-Cambrian

TABULAR VIEW OF THE PLANT KINGDOM

Phylum	Subdivision, Class or Order		Range	Common Name or Example
IV. Spermatophyta (Seed-plants)	Angiospermæ	Dicotyledones	Lower Cretaceous to present	oaks
		Monocotyledones	Lower Cretaceous to present	grasses
	Gymnospermæ	Gnetales	(Fossil record scant)	Ephedra
		Coniferales	Permian to present	pines
		Ginkgoales	Permian to present	Ginkgo
		Cordaitales	Devonian to Permian	Cordaites
		Cycadales	Permian to present	cycads
		Cycadofilicales	Devonian to Jurassic	Neuropteris
III. Pteridophyta (Fern-plants)		Lycopodiales	Devonian to present	club mosses
		Equisetales	Devonian to present	horsetails
		Sphenophyllales	Devonian to Permian	Sphenophyllum
		Filicales	Devonian to present	ferns
II. Bryophyta (Moss-plants)		Musci	Devonian? Tertiary to present	mosses
		Hepaticæ	Devonian? Tertiary to present	liverworts
I. Thallophyta (Thallus-plants)		Fungi	Silurian to present	fungi
		Myxomycetes	Fossil record lacking	slime-molds
		Schizomycetes	Proterozoic to present	bacteria
		Algæ	Proterozoic to present	seaweeds
		Diatomeæ	Jurassic to present	diatoms
		Cyanophyceæ	Archeozoic to present	blue-green algæ

TABULAR VIEW OF THE ANIMAL KINGDOM

Phylum		Class (or Subphylum)	Range	Common Name or Example
XIII. Chordata	Vertebrata	Mammalia	Triassic to present	mammals
		Aves	Jurassic to present	birds
		Reptilia	Pennsylvanian to present	reptiles
		Amphibia	Devonian to present	amphibians
		Pisces	Devonian to present	fish
		Elasmobranchii	Upper Silurian to present	sharks
		Placodermata	Devonian	Pterichthys
		Cyclostomata	Devonian ? to present	lampreys
		Ostracodermi	Ordovician to Devonian	shield-fish
	Invertebrata	Cephalochorda	(Fossil record lacking)	Amphioxus
		Tunicata	(Fossil record lacking)	ascidians
		Enteropneusta	(Fossil record lacking)	Balanoglossus
XII. Arthropoda		Insecta	Pennsylvanian to present	insects
		Arachnida	Cambrian to present	spiders
		Myriopoda	Devonian to present	centipedes
		Onychophora	Cambrian ? to present	Peripatus
		Crustacea	Cambrian to present	lobster
XI. Mollusca		Cephalopoda	Cambrian to present	Nautilus
		Scaphopoda	Ordovician to present	tooth shells
		Gastropoda	Cambrian to present	snails
		Pelecypoda	Cambrian to present	clams
		Amphineura	Ordovician to present	chitons
X. Molluscoidea		Brachiopoda	Cambrian to present	brachiopods
		Bryozoa	Ordovician to present	bryozoöns
IX. Echinodermata		Holothurioidea	Cambrian to present	sea cucumbers
		Echinoidea	Ordovician to present	sea urchins
		Ophiuroidea	Ordovician to present	brittle-stars
		Asteroidea	Cambrian to present	starfish
		Crinoidea	Ordovician to present	sea lilies
		Blastoidea	Ordovician to Permian	sea buds
		Cystoidea	Cambrian to Permian	cystoids
VIII. Annelida		Classes are omitted	Cambrian to present	segmented worms
VII. Trochelminthes			(Fossil record lacking)	wheel worms
VI. Nemathelminthes			Cambrian ? to present	thread worms
V. Platyhelminthes			Pennsylvanian to present	flat worms
IV. Ctenophora			(Fossil record lacking)	comb-jellies
III. Cœlenterata		Anthozoa	Cambrian to present	corals
		Scyphozoa	Cambrian to present	jelly-fish
		Graptozoa	Cambrian to Mississippian	graptolites
		Hydrozoa	Cambrian to present	hydrozoöns
II. Porifera		Spongiæ	Pre-Cambrian to present	sponges
I. Protozoa		Infusoria	(Fossil record lacking)	infusorians
		Sporozoa	(Fossil record lacking)	Gregarina
		Mastigophora	Cretaceous ? to present	Euglena
		Sarcodina	Pre-Cambrian to present	Amœba

PLANTS

INTRODUCTORY

THE continued existence of such life as is familiar to us depends upon the acquirement of external energy. At the surface of the earth the most available source of energy is the sun's rays. These acting through the chlorophyll — the green coloring matter of plants — break up the inorganic components of earth, air, and water into their separate elements and then recombine them into the potential, or stored-up, energy of foodstuffs. Plants expend this energy largely in reproduction — in the development of spores and seeds. Animals, on the other hand, make use of this energy stored up by the plants, expending it in free movements as well as in reproducing their kind. In the lowest divisions of each kingdom, however — the thallophytes of the plants and the protozoöns of the animals — still occur individuals, such, for example, as the protozoön, Euglena, which combine both methods of energy getting, and are in this respect transitional between plants and animals.

The **food** of plants consists principally of inorganic salts and carbon dioxide in solution in water; these are absorbed by the protoplasm of the plant. In the case of the unicellular plant, the whole plant body, being surrounded by the food, absorbs it, while among higher plants the roots and rootlets are differentiated to perform that function. In the lower plants (Thallophytes) the whole plant body is more or less completely immersed in water. Since water contains dissolved food, all the plant cells in contact with it absorb what they need. This sap (water and food) is transferred to bordering cells by osmosis through the thin cell walls. Thus in the thallophytes, as also in the bryophytes, the sap goes in a haphazard manner from cell to cell, like water oozing through a swamp.

Among higher plants, roots and rootlets are developed to perform the function of the intake of food material. This sap is then carried up to the leaves through cells arranged end to end forming pipe-like tubes but with cell walls at intervals. These tubes are arranged in bundles for strengthening (vascular bundles), as can be seen in a strand from a corn stalk (Figs. 17, 18).

In these higher plants the water and dissolved food is raised principally by transpiration pull and water cohesion, *i.e.*, the loss of water by transpiration from the cells of the leaves and stems tends to keep a higher concentration here, which results in withdrawing water from the bordering cells and so on down the plant. The result is the presence of continuous columns of water extending from the leaves to the roots. Each column is capable of holding together in the narrow cellular tubes because of its own cohesive force. The upward movement of water is also aided by root pressure — the pressure caused by the absorption of water by the roots, and also to some degree by capillarity. This upward movement is seen in the continued flow of sap after the main stem of a plant has been cut off.

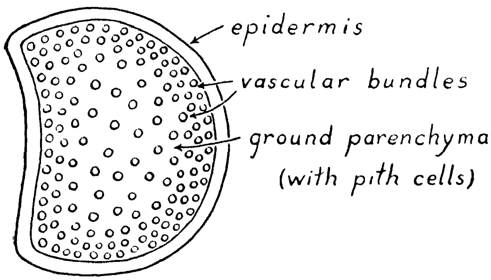


FIG. 17. — Diagrammatic cross section of the stalk of corn (Zea mays).

Under the influence of sunlight the carbon dioxide is broken up into the gases carbon and oxygen; the former after being combined with the inorganic substances is transferred to the growing parts of the plant through other tubes in the vascular bundles, while the oxygen is thrown off. This process is called photosynthesis, *i.e.*, the formation of carbohydrates and oxygen from carbon dioxide and water, through the action of light upon

living chlorophyll-bearing cells. The molecules of carbon dioxide (CO_2) and water (H_2O) are thus broken up into their respective atoms C, O, and H, and then recombined into carbohydrates, such as glucose and cellulose. $6\ CO_2 + 6\ H_2O +$ 677.2 calories from the sun become, through the action of chlorophyll, $C_6H_{12}O_6$ (glucose) $- O_{12}$ (waste). Glucose $- H_2O =$ $C_6H_{10}O_5$ (cellulose). Parasitic plants, such as the fungi and

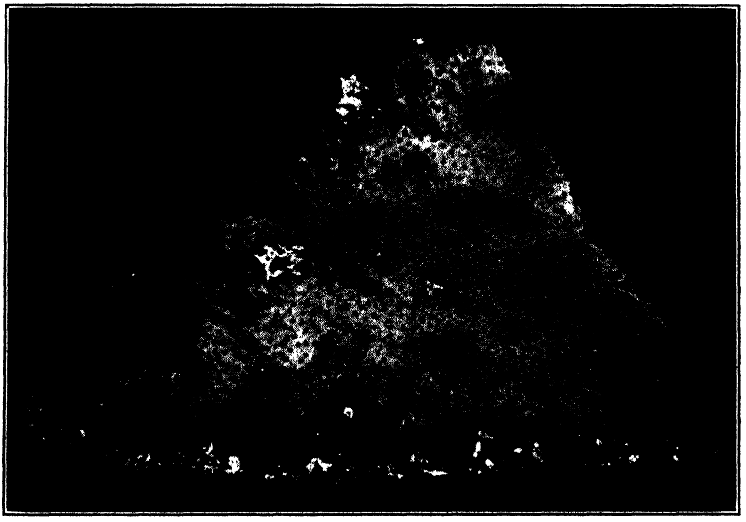


FIG. 18. — Cross section of trunk of a fossil palm (Palmoxylon) from the Cretaceous of India. Natural size. Replaced by silica. Compare with Figure 17.

bacteria, are exceptional in that they absorb the food directly from the host, either plant or animal, which has manufactured it.

Respiration. — Primarily all intake of oxygen and expulsion of carbon dioxide must take place through the cell wall, whether in plants or in animals. In the simpler water-dwelling plants this is the only method. In land plants, however, a cuticle has been developed which prevents too rapid evaporation of the water content of the cells. In these plants respiration takes

place partly through the cuticle but mostly through specially evolved stomata (small openings), which are especially abundant on the under surface of leaves, averaging 5,000 to a square centimeter. The use made of the oxygen is shown in the rise of temperature and in the energy of growth. An illustration of the rise in temperature in living plants is seen in such a form as the blue *Soldanella alpina* of the Swiss Alps. In spring when water trickles underneath the ice and down its rootlets, growth is aroused in the sleeping plant, and, through oxidation of the carbohydrates within its thick leaves, it melts its way upward through the ice. Since respiration is, in plants as well as in animals, a breaking down process, a waste product, carbon dioxide, is thrown out.

Reproduction among plants may be either sexual or asexual. Asexual plants reproduce either by simple division, as among the bacteria, or by merely detaching single cells from themselves, as among certain algæ; each of these detached cells, called in the latter case a spore, is capable of developing without fertilization into an independent plant. In sexual reproduction the plant likewise separates from itself certain single cells, but these cells lack the power of developing by themselves; before growth can occur each must unite with another cell, either from a separate plant or from different parts of the same plant. The larger of these complementary reproductive cells in the higher plants contains the egg and is the female; the other cell, which may or may not be free-swimming, contains the male element. In all except the seed-plants the presence of external fluid water is a necessity, otherwise the male cell cannot travel to the female and produce fertilization.

Plant organs. — Thus, just as the human body is made up of a variety of organs — eyes, hands, lungs, etc., — so the plant has organs to meet its needs — the stomata which give off carbon dioxide and water vapor and take in oxygen, the green chlorophyll which utilizes sunlight and manufactures starch, etc., roots, stem, and leaves. The tubes in the vascular bundles are utilized for the transference of raw material from the roots

to the leaves and of manufactured products from the leaves to other parts of the plant. There are also particular parts for reproduction and for protection. It is only in the higher groups of plants that these organs are differentiated; in the simplest plants, as in the simplest animals, the entire organism, usually microscopic, performs all these functions in a very generalized manner, without separate organs. From the simplest water-dwelling plants and animals to the higher land dwellers, there is an increasing subdivision of labor through the development of organs better adapted to the performance of necessary functions.

Resistance to freezing. — In plants, as in insects, it is the lower water content in winter which reduces the likelihood of freezing. During summer the sap in plants is relatively thin and easily frozen, but as cold weather approaches, the starch in the leaves of evergreens is converted into sugar and oil, changing the sap to a syrupy emulsion which is very difficult to freeze. In the Northern Hemisphere, the greatest density is usually reached during late January. Deciduous trees show some thickening of the sap in the leaves but this is withdrawn into the tree before the leaves fall, for the sap in the leaves just fallen freezes more easily than does that from leaves not quite ready to fall.

Plants as indicators of climate. — Plants, at least the later ones, are excellent criteria of climatic conditions; their inability to migrate under the stimulus of the annual alternation of cold and warm, wet and dry seasons makes them more valuable than animals as geologic thermometers. But that in the Mesozoic, and especially in the Paleozoic, geographic distribution was as sharply limited by climatic environment as now is unlikely. Some persistent primitive types such as the common brake (Pteris), which thrive in both temperate and tropical regions, are suggestive in this connection. The world-wide distribution of the ancient floras may have been mainly due to their primitive and generalized structure; they had not yet specialized to climatic environments.

Preservation of plants. — There are of necessity many gaps in the record left by the vegetation of past ages. The early plants were soft and perishable. Moreover, it is predominantly water life — the life of the sea beaches and the inland lakes and swamps — which has been preserved in the fossil state, since land conditions favor decomposition and destruction and do not furnish the conditions necessary to fossilization. It must accordingly be only a very incomplete idea of the past vegetation of the earth that fossil plants can furnish. Despite, however, the exigencies of fossilization, all the great groups of living plants — thallophytes (algæ, fungi), bryophytes (mosses, liverworts), pteridophytes (ferns, horsetails, club-mosses), and spermatophytes (gymnosperms, angiosperms) — have left a fossil record of the larger outlines of their past history. Plant evolution has not been uniform and there are many cases of retrogression, as in the club-mosses and horsetails, yet in general a higher group has succeeded a lower one, the latter not disappearing but falling into the background. Following the early Paleozoic, or age of seaweeds, spore-bearing plants and primitive gymnosperms dominated in the Upper Paleozoic. More modern gymnosperms and the cycadaceous or proangiospermous types made up the still cosmopolitan forest facies of early and mid-Mesozoic time, while from the Cretaceous to the present the angiosperms have been the leading type.

Classification of plants. — Reproductive organs are less influenced by environmental conditions than are vegetative organs. The closely related strawberry and raspberry, for example, have very dissimilar stems and leaves but their flowers are constructed on the same general plan. Hence it is that plants are divided primarily on the basis of their method of reproduction, secondarily on such vegetative organs as cellular and vascular structures, stem, and leaves. Until systematic botanists have come nearer to an agreement upon the great groups of plants, the old classification of the Plant Kingdom into the four divisions or phyla given below will continue to be widely used. Into these divisions are placed the 233,000

species of living plants and the innumerable fossil species, though among the latter are many transitional groups difficult of classification.

CHAPTER II

PHYLUM I. THALLOPHYTA

The thallophytes include the most primitive plants, ranging in size from single microscopic cells to seaweeds of enormous dimensions. The forms included in this group agree in their simple structure, being plants in which there is little or no differentiation of organs, such as stems and leaves. Such a simple plant body is called a thallus, and the plants distinguished by possessing this undifferentiated mass of cellular tissue are called the thallophytes or thallus plants (> Greek thallus, young shoot + phyton, plant).

The Thallophyta may be separated into two artificial subphyla, based upon the manner in which the plants secure their food.

SUBPHYLUM 1. AUTOPHYTIC THALLOPHYTES

Since these have chlorophyll, they are able to carry on photosynthesis and can thus live upon inorganic matter. They include the three classes:

A. Blue-green algæ
B. Diatoms
C. Algæ.

CLASS A. BLUE–GREEN ALGÆ (CYANOPHYCEÆ)

These are unicellular plants, without definite nuclei, occurring often in colonies held together by a jelly-like material. They possess a blue pigment in addition to chlorophyll. A red pigment is also present in some forms, like *Trochodesmium erythraeum*, which at times flourishes in enormous numbers in the

Red Sea, giving a bright red color to the water. Some blue-green algæ secrete lime, and are thus important as rock builders. They have been reported from the Archeozoic to the present.

CLASS B. DIATOMS (DIATOMEÆ)

The diatoms are a group of thallophytes with possible kinship to green and brown algæ. They are microscopic, chlorophyll-bearing, one-celled plants, with a distinct nucleus. Each diatom is inclosed in a wall consisting of two valves, one of which overlaps the other like the cover of a cardboard box. This cell wall is impregnated with silica in the opal condition; it is frequently of a beautiful pattern. Reproduction is either asexual, through the division of the cell, each half taking one valve and secreting another, or sexual through the union of two cells which escape from their valves to form a new individual (Fig. 19).

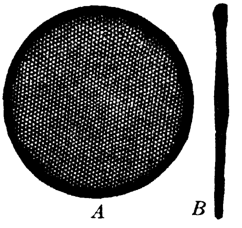


FIG. 19. — Examples of the silica-secreting algæ, *diatoms*, abundant in the ocean covering eastern Maryland during the Miocene (Calvert) times. *A*, *Coscinodiscus lineatus* Ehrenberg, a circular species. *B*, *Sceptroneis caduceus* Ehrenberg, a lanceolate species. Each × 170. (From Boyer.)

Diatoms occur in both fresh and salt water as well as in damp soil. In the ocean they form a large part of the plankton, the drifting mass of organisms at the surface of the water, and furnish the food of many marine animals. There are at times 200 diatoms to each drop of water at the surface, and they extend in large numbers to a depth of probably 20 meters. Because of their chlorophyll, diatoms make use of the sunlight to utilize the dissolved inorganic substances in the water. Since it is upon these diatoms that fish feed, either directly by means of gill rakers or indirectly through minute crustaceans, etc., which feed upon diatoms, there has arisen the expression, "all fish is diatoms." Exceptionally clear skies in the North Atlantic ocean are followed by cheaper fish two years later in the neighboring markets.

The skeletons of diatoms cast off at death or in the process of reproduction form on the ocean bottom or on the bottom of ponds or marshes deposits of siliceous earth — the diatomaceous ooze. When this becomes solid rock it is called diatomite.

CLASS C. ALGÆ

The algæ, commonly known as seaweeds, are primitive, water-dwelling plants, ranging from microscopic, one-celled forms to large and complex plants. The majority live submerged in salt or fresh water; practically all the others are found on wet substrata, or at least carry on an active existence only during the periods when moisture is abundant (*e.g.*, Protococcus). The green coloring matter (chlorophyll) always present is masked in certain of the algæ by brown and red pigments.

There is great variety in the method of reproduction. It may be either asexual through the production of special cells, the spores, which later develop into new plants, or sexual through union of male and female cells. Upon other structural and reproductive characters coupled with the difference in color is based the classification into green, brown, and red algæ. Algæ have been recognized from the pre-Cambrian to the present.

1. Green algæ. — Unicellular and multicellular. Common examples are:

1. The unicellular green Protococcus abundant on the sides of rocks and shaded trees in the North and South Temperate zones. This is probably the commonest green alga in the world and is remarkably resistant to drought.

2. The unicellular desmids abundant in fresh water. The multicellular Spirogyra in which the cells are arranged end to end, forming long filaments. The accumulation of these algæ forms "pond scum."

3. Halimeda, a lime-secreting alga of modern seas. It grows on coral reefs, connecting dead coral masses. It forms extensive limestone deposits in the lagoons of coral atolls, as in the Funa-

futi reef. The analysis of the plant, which gives over 90 per cent of lime and only $3\frac{8}{10}$ per cent of organic matter, shows its importance as a rock builder.

4. Chara (stonewort). (There is a growing tendency to remove Chara from the green algæ and to raise it into a distinct group.) This plant inhabits fresh-water lakes of the temperate region. It secretes lime with which it encrusts its leaves and stems, even penetrating their superficial membranes, making them white and brittle. Upon the death of the protoplasmic part of the plant, this lime deposit disintegrates and settles as a limy mud, the marl of marl ponds. Chara is responsible for many fresh-water limestones of the past. Characteristic spore cases (oögonia) occur in the mid-Devonian at the Falls of the Ohio and in the Hamilton of Missouri, and are well known since the Upper Jurassic. It was especially abundant in the Tertiary. On the Isle of Wight there are considerable deposits of Oligocene fresh-water limestone which are rich in remains of Chara.

2. Brown algæ. — Examples are:

1. Fucus, the rock weed, common on rocks exposed between tides.

2. Laminaria, the large alga, devil's apron, etc., growing in the deeper water beyond the low tide limits (Fig. 23, *A*). This marine genus includes the largest plants known, some having huge trunk-like stalks and reaching a height of several hundred feet.

3. Sargassum of the Sargasso seas.

4. Nematophycus, a large plant whose fossilized stems have been found in the Silurian and Devonian of Europe and America. In some respects it resembles the big Laminarian seaweeds of the present, though its exact relationship cannot be determined since its microscopic structure is not preserved.

There are no important lime-secreting genera among the brown algæ.

3. Red algæ. — The lime-secreting types of these algæ are the "nullipores" or "corallines." They include among others:

1. Corallina. This plant grows in delicate jointed filaments which form little tufts on rocks and seaweeds in tide pools along the northern Atlantic coast. The white incrustation of its fronds gives it a coral-like appearance. Primicorallina is a distantly related form from the Ordovician (Fig. 20).

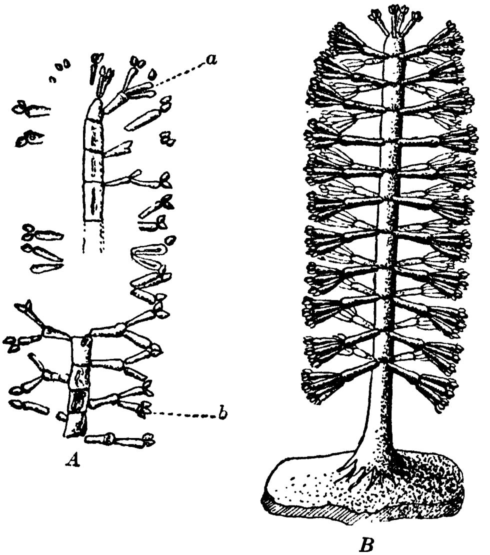


FIG. 20. — A marine lime-secreting alga, *Primicorallina trentonensis* Whitfield, from the Trenton limestone (Middle Ordovician) of New York. Much of the limestone where it occurs is made up of its remains. *A*, a specimen showing the whorled arrangement of the branchlets of the second order at *a* and those of the third order at *b*. *B*, restoration of the entire plant. (From Ruedemann.)

2. Lithothamnion. The precipitate of lime deposited by this plant usually forms crusts on the surfaces of shells, corals, and rocks on which it grows (Fig. 21). On the coast of Spitzbergen, for example, it covers the bottom in deep layers for many miles, the material for future strata ot the earth's crust. Some globular arctic species reach a diameter of six to eight inches. Lithothamnion has been one of the principal reef builders since the Cretaceous.

3. Here also may probably be placed such early Paleozoic calcareous masses as Cryptozoön (Fig. 21).

4. Doubtful algæ. — It has been shown that many fossils which were formerly described as algæ are not plants. Some are the molds of burrows or tracks of animals and some are of inorganic agency, such as Oldhamia from the Cambrian of Ireland,

formerly considered one of the oldest examples of vegetation and now explained as merely the wrinkling of the slate due to pressure. The "Cockstail alga" (*Taonurus cauda-galli*) which occurs in great abundance in the "Cauda galli grits" (Esopus) of the Middle Devonian of New York, and *Arthrophycus alleghenensis* (*harlani*) abundant in the Medina sandstone of the

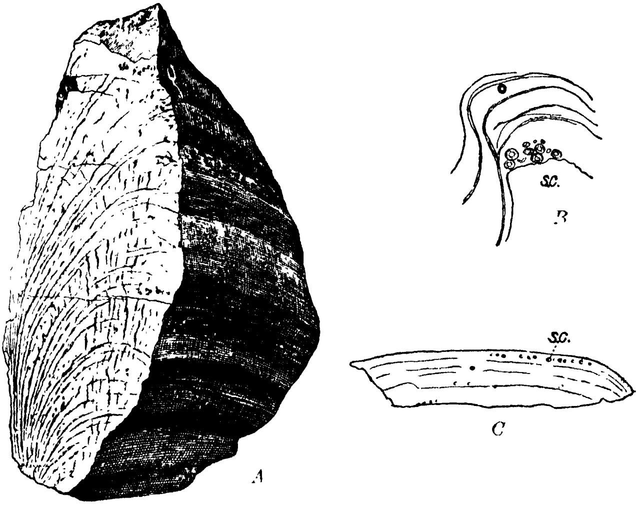


FIG. 21. — Comparison of the ancient Cryptozoön with the modern alga, Lithothamnion. *A*, *Cryptozoön bassleri* Wieland (× $\frac{1}{6}$), from the Cambrian of Pennysl vania. The vertical transverse section shows the successive laminæ of growth. *B*, *Cryptozoön proliferum* Hall, from the Beckmantown (Lower Ordovician) of Pennsylvania. The transverse section (× 6) shows what may be spore cases (*s.c.*). *C*, *Lithothamnion* living off the coast of Eastport, Maine. The vertical transverse section (× $1\frac{1}{2}$) shows the growth laminæ and the spore cases. (*A* and *B* after Wieland.)

Silurian, are at present generally regarded as the burrows of chætopod worms.

SUBPHYLUM 2. HETEROPHYTIC THALLOPHYTES

These plants are especially distinguished by the absence of chlorophyll. Since without this they cannot carry on photo-

synthesis, their principal source of energy is, as in animals, the organic. Accordingly, they live either as saprophytes upon decaying organic matter, or as parasites upon living organisms. Without the action of these plants in causing the decay of dead organisms, the surface of the earth would be covered so deeply with the dead bodies of plants and animals that life must cease to exist. The name (>Greek *heteros*, other or different + *phyton*, plant) refers to the different method of getting energy from that usual among plants.

These are subdivided into the three classes:

A. Bacteria
B. Slime fungi
C. Fungi.

CLASS A. BACTERIA (SCHIZOMYCETES)

The bacteria are simple, one-celled plants, without definite nuclei. They average about two microns in diameter. Within this minute plant body are carried on all the life activities. When the water surrounding it contains much food, the plant will grow to a certain maximum size and then divide by fission into two bacteria of equal size.

Bacteria are of three principal shapes, the sphere (coccus), the rod (bacillus), and the spiral (spirillum). These are of great economic importance as agents of fermentation, decay, and disease; they are now the chief agents in the decomposition of organic matter and unquestionably were similarly active in disintegrating the dead organisms of at least later geological ages, as is indicated by fossil evidence. Certain fossilized plant tissues of the Pennsylvania coal-beds show a destruction of cell walls which has been ascribed to this cause. But for their activity it is probable that ancient plant and animal remains would have been preserved in greater abundance. Since they have been found in the coprolites (fossil fæces) of fish, amphibians, and reptiles of the Permian, it can be concluded that they had by this time become parasitic in the alimentary canal of vertebrates.

Bacteria are known as fossils from the Proterozoic to the present.

The bacteria and the blue-green algæ are often grouped together in the phylum Schizophyta.

CLASS B. SLIME FUNGI (MYXOMYCETES)

The slime-moulds are sticky masses inclosing many nuclei but without cell walls. They frequently occur on decaying logs and leaves in a forest. They so combine the characters of plants and animals as to make it doubtful with which they should be classed. They live upon decaying organic matter, have locomotion like Amœba, and possess no chlorophyll, but they are terrestrial (sub-aërial) in habit and in their reproduction they are very much like certain fungi. After locomotion ceases, slender stalks arise with an enlarged upper portion in which the spores are formed. The spores have cellulose walls, another plant characteristic.

Slime fungi are not known as fossils. Living examples are Stemonitis and Arcyria, common on decaying wood.

CLASS C. FUNGI

Instead of possessing the more complex structure of chlorophyll-bearing plants, a fungus consists essentially only of a branching mass of threads called the mycelium (*e.g.*, the cobwebby rootlets of a mushroom). These threads penetrate the cell walls of their " host " — plant or animal — and live upon its substance. There is also the spore-bearing portion ; *e.g.*, the edible part of the mushroom. The fungi are divided into the algal fungi (Phycomycetes), including the bread mould and grape mildew, the sac fungi (Ascomycetes), represented by the powdery mildews and yeasts, and the club fungi (Basidiomycetes), the highest of the fungi, to which belong the rusts, smuts, toadstools, mushrooms, bracket fungi, and puff balls.

As would be expected from their structure, fungi are rarely preserved as fossils. Mycelial threads of a fungus have been

detected under the bark of Sigillaria from the Pennsylvanian coal-beds, and there is evidence that even as far back as the Silurian, fungi preyed upon " shell-fish," since certain brachiopod shells are found more or less perforated by fine tubules which in some cases end in spherical swellings. These borings (Fig. 22) are probably the work of the mycelium of a mould-like fungus (Phycomycete).

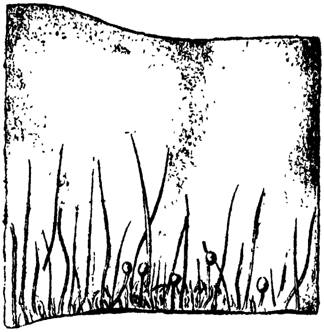


FIG. 22. — A *fungus* penetrating an impunctate brachiopod shell on one side only. The round swellings were probably spore sacks. This fungus from the Clinton (Silurian) of Rochester, New York, is probably a member of the Phycomycetes. × 250. (After Loomis.)

Lichens are thallophytes of wide distribution. They are dry gray and brown fronds spreading over tree trunks and rocks. They represent a union of algæ and fungi, since each lichen is actually made up of a fungus and an alga, living together in the mutually helpful relationship called symbiosis. The threads or mycelium of the fungus interweave among the minute cells of the alga, producing a comparatively long thallus, the lichen. The fungus also aids in absorbing water from the substratum or moist air and passing it on to the alga; it also aids the algal cells from fatal drying out during dry spells. The algal cells manufacture all the food for the colony.

The fungus belongs usually to the Sac fungi and the alga to the blue-green algæ or to Protococcus and its allies of the green algæ. In some cases it is possible to raise the alga and fungus separately; if they are later brought together, the fungal threads inclose the algal cells, producing the lichen.

Fossil lichens have been recognized only from very recent formations.

Thallophytes as Rock-Builders

The only living substance in plants, as in animals, is the jelly-like protoplasm. This must be protected and supported if the plant is to increase in size beyond the microscopic. The substance nearly universally manufactured is cellulose, the familiar woody fiber. This is deposited in the crystalline condition, and is frequently reinforced by a deposition of lime carbonate or of silica. It is in the securing of carbon from the decomposition of CO_2 for the building of their tissues that thallophytes secrete lime. Land plants derive the CO_2 from the air. Aquatic plants must secure it from the water. An excess of CO_2 in the water holds lime carbonate in solution, and when the CO_2 is abstracted from the water by the plants, the lime is of necessity thrown down, and thus is deposited in or upon the tissues of the plant which caused its precipitation. Some submerged plants, such as various groups of algæ, are particularly noteworthy for such deposition.

Algæ as rock-builders. — Algæ have been found to be in many cases, at least, the most important lime contributors to the upbuilding of the coral reefs, much more important than the corals themselves. A boring in the atoll of Funafuti penetrating to a depth of 1114.5 feet showed that in the composition of this typical "coral-reef" the order from most to least abundant of the most common organisms is as follows: (1) Lithothamnion; (2) Halimeda; (3) Foraminifera, a lime-secreting order of Protozoa; (4) Corals. All these occurred from top to bottom of the boring. Thus in the formation of this atoll nullipores were found to be the most important agent. This is true to a greater or less degree of many other "coral-reefs" of the Pacific Ocean, also of the East Indian and West Indian waters and the Mediterranean. Of these nullipores, Lithothamnion grows abundantly at a depth of two to three hundred fathoms; it also occurs in waters far from the tropics; off the coasts of Spitzbergen and Nova Zembla it covers the bottom in water of ten to twenty fathoms. The growth of nullipores may be

faster than that of corals since they often cover and smother living colonies of the latter. Lime-secreting algæ are thus seen to be of vast geologic importance in the formation of limestones since they grow so rapidly and at such various depths and temperatures. But evidences as to the nature of the organisms which build the limestone may be destroyed. The studies of J. Walther on a Lithothamnion reef at a depth of one hundred feet in the Bay of Naples have shown that diagenesis (*i.e.*, the movement of the waters contained in the reef, the action of microörganisms and recrystallization) may obliterate all the structure of the seaweed, leaving a structureless limestone. Many examples of such structureless limestones are known from the Mesozoic and Cenozoic rocks of southern Europe, in some of which a few specimens of Lithothamnion are still preserved. Thus it may not always be possible to tell in the study of any given limestone what organisms were operative in its upbuilding. In those cases, however, where the species can be recognized, calcareous algæ are often valuable as index fossils since there are certain forms with restricted geological, but wide geographical, range. Such, for example, is *Solenopora compacta*, abundant during the Middle Ordovician in Canada (Trenton and Black River formations), in Scotland (Llandeilo-Caradoc), and in northern Europe. It often forms entire beds of limestone; at times it weathers out as little pealike masses.

The lime precipitated by modern algæ is relatively high in magnesium carbonate. If this was equally true of algæ of past ages, it may account in part for the general dolomitization of limestones.

Algæ have been very important rock-builders from the Proterozoic to the present. Only a few examples can be noted. Reef structures in the Bighorn dolomite (Upper Ordovician) of Wyoming are probably due to these. In the Van Horn region of Texas, there are in the Permian, limestone and dolomite reef barriers, at times thirty miles in length and with a thickness of three thousand feet. They consist largely of algæ, but these are accompanied by sponges, bryozoöns, corals, and thick-

shelled brachiopods. These barriers separated a lagoon containing many fusulinid protozoöns from an open sea in which were many bryozoöns and brachiopods. The weathered surface of the gigantic reefs, at times over three thousand feet thick, in the Triassic dolomites of southern Tyrol, seem to indicate that they too were largely built up of calcareous algæ.

Certain algæ, the thermal algæ, are responsible for the beautiful siliceous and calcareous deposits of the Yellowstone Park. In some way not wholly understood they cause the deposition of the calcium, as at Mammoth Hot Springs, or of the silica, at most of the other hot springs. The beautiful colors of these deposits are hence due to plants — plants which here live in water of a very high temperature — between 90° and 185° F. The kind and color vary with the temperature, there being representatives of the green algæ, the blue-green, etc. In the cooler waters these forms may be recognized as algæ, appearing in green filaments, or red or brown leathery sheets lining the springs and resembling the seaweeds of the coast. But in the hotter springs the masses become so densely gelatinous, or so thickly encrusted with silica, as not to be easily recognized.

In *diatoms* the cellulose cell wall is so impregnated with silica (opal) as to form a resistant skeleton. In the present oceans diatoms are most abundant in waters of low salinity (Antarctic and Arctic oceans). Hence diatomaceous ooze is found most extensively in the cold temperate and polar regions of the Northern and Southern Hemispheres. Such deposits are recorded from the Tertiary to the present. The Monterey shale (Miocene) of California is, in some localities, composed largely of diatoms. Fresh water deposits are also abundant.

Some *bacteria* are probably an important agent in precipitating lime muds. There are also iron-depositing bacteria and those that deposit sulfur.

1. What is the source of the energy of plants? of animals?
2. How do plants take in food? What is this food?
3. Distinguish between thallophytes and higher plants in the manner of food-getting.

4. How is sap raised to the top of a tall tree?

5. What is the difference in the respiration of a water-dwelling thallophyte and a higher land plant?

6. Describe photosynthesis.

7. Briefly describe reproduction in plants.

8. Enumerate some plant organs and illustrate subdivision of labor.

9. How do plants prepare for winter so that they keep from freezing?

10. How are plants good indicators of climate?

11. Compare plants and animals (*a*) as indicators of climate; (*b*) as to likelihood of preservation as fossils.

12. Upon what bases are plants classified? List the four phyla.

13. Define thallophytes. What is the significance of the name? What is the basis for their subdivision into two artificial subphyla?

14. What are the blue-green algæ? What is their geologic range? Cite a living example.

15. Describe a diatom. Discuss the abundance, distribution, size, and economic importance of diatoms.

16. Describe some examples of green algæ; brown algæ; red algæ.

17. Of what importance are the heterophytic thallophytes in the economy of nature?

18. Describe bacteria. What is their importance in nature?

19. What evidence is there that some bacteria had become parasitic by the late Paleozoic?

20. Describe slime fungi.

21. What are the two essential parts of a mushroom?

22. Name some fungi that man has utilized.

23. What is the geologic range of fungi?

24. What are lichens? their geologic age?

25. Why is a protective wall necessary to a water-dwelling thallophyte? Of what material does this wall consist?

26. Could a plant whose cell walls consisted entirely of lime or silica live, *i.e.*, carry on photosynthesis?

27. How is lime secreted by algæ?

28. Show the importance of algæ as rock-builders to-day; in the past.

29. How may an organic limestone reef be rendered structureless soon after its deposition?

30. Where do diatomaceous oozes occur most abundantly to-day?

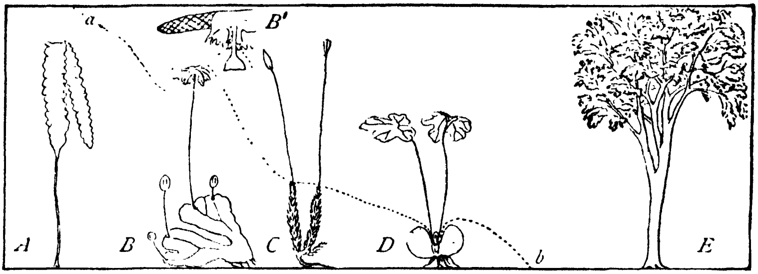
31. How do bacteria aid in rock-building?

CHAPTER III

PHYLUM II. BRYOPHYTA

The Bryophyta exhibit a distinct advance upon the Thallophyta in their terrestrial habit, the greater specialization of the plant body and in the constant occurrence of alternation of generations in the life cycle. As the algæ are essentially water-dwelling plants, there is little necessity for specialization of organs since any of the plant's cells can serve for absorbing the food which surrounds it on all sides. With the evolution of the bryophytes there came a change from aquatic to terrestrial conditions and there thus arose the need for specialized organs adapted to getting food from the soil and from the air. The not very efficient root-like hairs, called rhizoids, take water and other necessary substances from the soil. To protect against excessive loss of water, the cells at the surface of the plant are provided with a cuticle which is lacking in the Thallophytes. The adaptation to terrestrial conditions being still imperfect, however, many of the bryophytes, such as some of the liverworts, still have thalloid plant bodies, while the group as a whole is moisture-loving (Fig. 23, *B*, *C*). During very dry periods they almost cease vegetating.

The most distinct advance, however, of the bryophytes upon the thallophytes is in the method of reproduction — in the establishment of a distinct alternation of generations. This method is illustrated by the life history of some common mosses, such as the hair-cap (*Polytrichum commune*, Fig. 23, *C*). This plant, as we commonly see it, consists of a green stalk bearing many tiny leaves, and, if the plant is fruiting, it supports at its apex a slender bristle-like seta which ends in a sac (capsule) containing spores. When the spores fall on moist earth they may



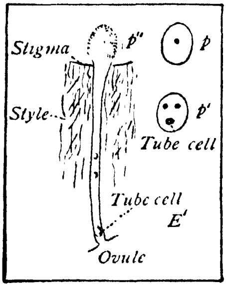


FIG. 23. — Diagram to show the increase in prominence of the sporophyte stage of plant life from the algæ to the higher seed-plants. Among the thallophytes, both the sexual and asexual methods of reproduction are represented. *A* illustrates the asexual, wherein certain cells of the plant divide into smaller cells, — the zoöspores, which, without union with other cells, develop directly into new plants. *B–B'* illustrate the sexual method effected through an alternation of generations, wherein a vegetative stage — the sporophyte — alternates with a reproductive stage — the gametophyte. The gametophyte stage of the various forms is below the line *a–b*, the sporophyte stage above it. The size of the plants in the diagram bears no relation to their size in nature. This diagram need not imply that the seed-plant has been evolved from the algæ successively through the mosses, etc.; the fern may have arisen more directly from the algæ, but it must have evolved from a small sporophyte stage to a large one, possibly through some such generalized stage as is preserved in the Rhynie bryophytes. *A*, the marine alga, *Laminaria saccharina*, the devil's apron. *B*, the very common liverwort, *Marchantia polymorpha*. *B'*, same, with the tip of one of the umbrella-like lobes magnified. *C*, the hair-cap moss, *Polytrichum commune*. *D*, a very young sensitive fern, *Onoclea sensibilis*. *E*, the elm tree, *Ulmus americanus*. *E'*, same, with the gametophyte stage enlarged. Among the bryophytes, *B* and *C*, the gametophyte is the prominent stage. This is the common liverwort or moss plant which bears the sporophyte; this latter remains attached to and dependent upon the gametophyte throughout its whole existence. In the pteridophytes, *D*, the sporophyte is the prominent, common, leafy fern plant which has become independent of the gametophyte. The latter is the true two-lobed prothallus which, though independent of the sporophyte, is tiny and short-lived. In the spermatophytes, *E*, the gametophyte stage has become so reduced that its whole existence is passed invisibly dependent upon and within the sporophyte. *p*, pollen grain with its single included nucleus; *p'*, the same at a later stage with three nuclei; *p''*, the same lodged upon the stigma, with the pollen tube already penetrating the ovule.

germinate by sending out a mass of green threads, the protonema, and from this grow the moss plants. Some of these plants bear at their summits the male and female reproductive organs, and from the union of their products, the fertilized egg cell, arises the spore-bearing part of the plant, *i.e.*, the capsule borne at the summit of the seta. Thus there is an alternation of the asexual or sporophyte stage — the product of the union of male and female elements — and the sexual or gametophyte stage — the product of the germination of the spores. This alternation of generations is characteristic of all bryophytes. The moss plant is distinguished by the predominance of the gametophyte stage over the sporophyte, since the sporophyte is only the slender stalk and its capsule, dependent on the leafy moss plant, the gametophyte.

Derivation of name. — Greek *bryon*, moss, + *phyton*, plant, referring to its typical class, the mosses.

The Bryophyta are divided into two classes — the liverworts (Hepaticæ) and the mosses (Musci).

CLASS A. LIVERWORTS (HEPATICÆ)

These include the simplest bryophytes, with many similarities to the algæ. Riccia and Marchantia are common examples. *Marchantia polymorpha* (Fig. 23, *B*) is the most common and widely distributed liverwort; the thallus averages one to three inches in length.

CLASS B. MOSSES (MUSCI)

Mosses are to-day much more abundant than liverworts. The haircap moss, *Polytrichum commune* (Fig. 23, *C* described above), and the peat moss, Sphagnum, are common examples.

In Sphagnum most of the leaves consist of many small chlorophyll-bearing cells and a few large empty cells with a circular opening. It is the empty cells which are responsible for the light green color of the leaves, and because of their presence the

Sphagnum has a great capacity for the absorption of water. It is thus one of the most important agents at present in the formation of peat. The plants live in bogs and as they die below they grow above. Their habitat is mainly sub-arctic to cool temperate.

It seems probable that the ancient representatives of bryophytes were more delicate than the modern forms, for only under exceptional conditions have they been preserved. In the early Devonian series of silicified peat beds at Rhynie, Scotland, occur many delicate plants, such as Rhynia and Hornea, which are interpreted as generalized bryophytes, with strong affinities for the algæ below them in the evolving line and with the ferns above them.

1. In what respects are the bryophytes an advance upon the thallophytes?
2. Describe both stages (gametophyte and sporophyte) of a common moss plant.
3. How far back in geologic time are fossil bryophytes found?
4. Name the two classes into which the Bryophyta are divided with an example under each.

CHAPTER IV

PHYLUM III. PTERIDOPHYTA

The pteridophytes are much more complex plants than the bryophytes. While the structure of the moss plant is more or less simply cellular, that of the fern plant is vascular; that is, like the higher flowering types, the plant possesses a series of vessels which form a conducting apparatus for the food and manufactured sap. Bryophytes and pteridophytes are sometimes called cryptogams; that is, plants without true flowers and seeds, in distinction to the phanerogams, or higher flowering plants; of these the bryophytes are the cellular cryptogams, and pteridophytes the vascular. Like the bryophytes, the pteridophytes reproduce by a conspicuous alternation of generations, but differ from the bryophytes in the relative importance of the sexual (reproductive) and the asexual (vegetative) stages. In both, the better-known and longer-lived part of the life history is represented by a leafy plant which alternates with a less conspicuous phase. The leafy moss plant, however, originates from the spore and produces male and female elements, while the leafy fern plant originates from the fertilized egg and produces spores. Thus, while the moss plant is the reproductive or gametophyte stage, the fern plant is the vegetative or sporophyte (Fig. 23, *D*). The life history of the Pteridophyta may be illustrated in general by observing the development of some ferns, such as the common Christmas fern. Some of its leaves will be found to bear shorter leaflets near their ends. Upon the under side of such leaflets are rows of small dots, the sori or heaps of spore cases. When one of the tiny spores drops to the ground under conditions where it can germinate, it develops into a small, flat, disk-like body, the prothallus. This is

nourished by its root-like hairs, the rhizoids. Upon the prothallus develop the male and female reproductive organs and from the union of their products, the fertilized egg, grows the leafy fern plant. For a short time this is nourished by the prothallus but quickly the fern plant develops a root which attaches it directly to the soil and thus enables it to get its own food supply. Thus, in ferns, the sporophyte, which is the leafy plant, and the gametophyte, which is the prothallus, are independent of each other. It has been seen that in mosses the sporophyte is dependent entirely on the gametophyte, and it will be seen later that in the higher flowering plants the gametophyte is completely dependent on the sporophyte.

Towards the development of a land flora, the pteridophytes represent an advance over the bryophytes in (*a*) the independence of the sporophyte generation, (*b*) the well-organized vascular system, (*c*) the more efficient epidermis, (*d*) the development of a root which can penetrate into the deeper and relatively moister layers of soil.

Derivation of name. — Greek *pteris*, fern, + *phyton*, plant, in reference to its best-known class, the ferns.

The Pteridophyta are sub-divided into the following classes:

A. Ferns (Filicales) (including Ophioglossales, which is sometimes considered a distinct class)
B. Horsetails (Equisetales)
C. Club-mosses (Lycopodiales)
D. Sphenophyllales.

CLASS A. FERNS (FILICALES)

The leaf or frond of the fern is generally broad and is often divided into leaflets (pinnæ). The spore cases are gathered into the round " fruit dots " (sori), borne on more or less modified portions of the leaves or on independent fruiting stalks (sporophyll) (Fig. 24, *B*).

Ferns are widely distributed over the earth. They flourish

most luxuriantly in moist, shady habitats. In size they vary up to fifty feet in height in some tropical tree ferns.

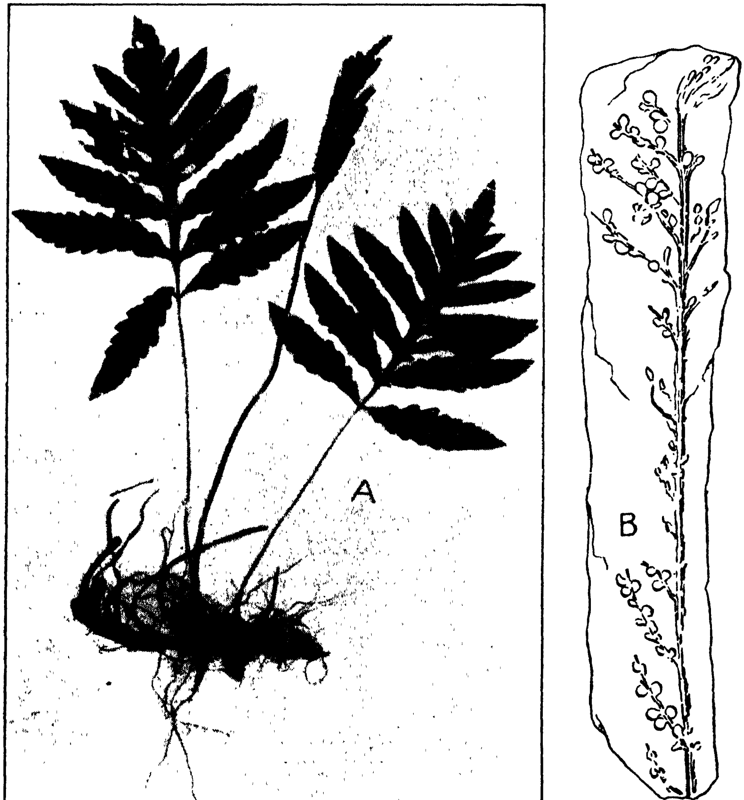


FIG. 24. — The fern, Onoclea. *A*, the living sensitive fern, *O. sensibilis* L. ($\times \frac{1}{4}$), from Maine; the fruiting stalk between two sterile leaves. *B*, *O. inquirenda* Hollick ($\times \frac{3}{4}$), from the Cretaceous of Long Island, New York; the fruiting stalk. (*B*, from Hollick.)

In the majority of ferns, the spores are all of one size, homosporous, each spore giving rise to a single prothallus. In the so-called water ferns, they are of two sizes, heterosporous, each giving rise to a prothallus, the small spores to male gametophytes

and the larger spores to female gametophytes. Common living examples of the former class are the Christmas fern (Polystichum), sensitive fern (Onoclea), and polypody (Polypodium); in the latter group are Marsilia and Salvinia.

Ferns are known to have existed from the time of the Devonian, and must have appeared before the close of the Silurian. Nearly all the living families have existed since the Jurassic, while at least two families, the Osmundaceæ and the Marattiaceæ, have been traced back to Paleozoic ancestors. It is rare that all of the organs of any fossil plant may be described, since they are so easily separable. Until recently the characterization of many fossil genera rested solely on the form and venation of the leaf. One of the largest of these frond genera was Neuropteris (see page 85). Fructifications later found in connection with leaves of this genus have determined that this as well as many other genera with fern-like fronds is not a true fern but a member of the great order of seed-ferns, an order of Spermatophyta intermediate between the ferns and the cycads.

Fossil examples of true ferns are:

1. Archæopteris. A tree fern which had a wide distribution throughout eastern North America and Europe during the Upper Devonian.

2. Osmundites (Jurassic to Tertiary). Fern stems with the peculiar structure of the stem of the living Osmunda, the common royal fern. This relationship is suggested by the name in which the suffix "-ites" added to the name Osmunda means "stony"; this suffix is used in many names of fossil plants to suggest their kinship with modern forms.

3. Dictyopteris and Camptopteris. Remarkably handsome forms of Upper Triassic-Cretaceous age, with lyrate fronds often three feet or more broad, and with a characteristic netted venation.

4. The sensitive fern (*Onoclea sensibilis*). Now living only in eastern North America and eastern Asia, but present throughout the Northern Hemisphere during the Pliocene. The genus was in existence during the Cretaceous (Figs. 23, *D*, 24).

1. How do the pteridophytes show an advance over the bryophytes towards the development of a land flora?
2. Give briefly the life history of the common Christmas fern.
3. Into what four classes are the Pteridophyta sub-divided? Give both scientific and common names.
4. With what ferns are you familiar? Have you ever seen a fern prothallus? Which is the more commonly seen stage of the fern — the reproductive or the vegetative?
5. When, in geological time, did ferns appear?
6. Name two fossil examples.
7. Distinguish between homosporous and heterosporous ferns.

CLASS B. HORSETAILS (EQUISETALES)

Living horsetails are low plants, growing usually in moist localities, but often on railway embankments. In the temperate regions the species range between one to five feet in height. They have simple or branching stalks which are strongly furrowed longitudinally, are divided into sections by very distinct joints (nodes), and have hollow internodes. The leaves are small papery scales, arranged around the stem in a circle at each node. Because of the papery leaves, photosynthesis is carried on largely by the stems. The outer tissue of the plant has a heavy impregnation of silica which gives it so hard a texture that it was formerly used for polishing metal utensils, and thus arose its name of "scouring rush." The fruit (strobilus) is a terminal cone. This is a stem with much shortened internodes. At the nodes the leaves (now called sporophylls) bear sporangia. (The flower of higher plants is also a stem which bears sporophylls.)

Derivation of name. — Equisetales is the Latinized form of the common name horsetail > *Equus*, horse + *seta*, a stiff hair. The much-branched vegetative (sterile) stalk looks like a horse's tail.

In the Carboniferous, representatives of this class were large forest trees and bore large leaves. These fossil remains show that horsetails were formerly one of the most abundantly represented groups of plants, though at present the class survives in only one genus, Equisetum, of which there are about thirty living species.

The Equisetales have existed from the Devonian to the present. Apparently the last of the Calamites group, the Paleozoic horse-tails, died out at the close of the Paleozoic; but in the Mesozoic

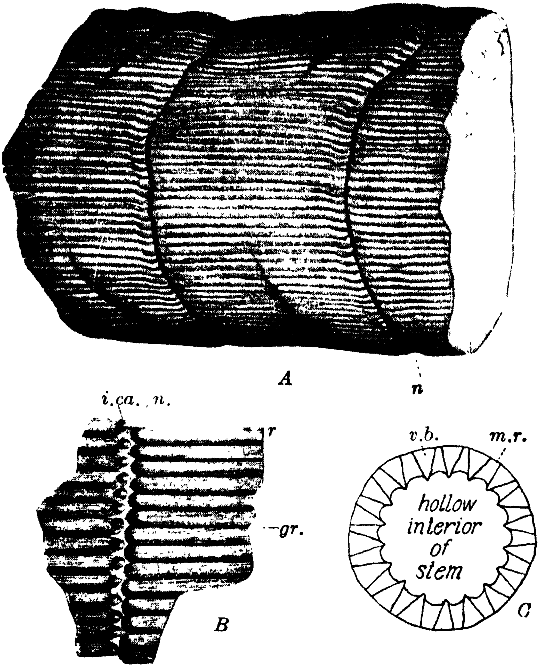


FIG. 25. — The ancient horsetail. *A*, *B*, *Calamites suckowi* Brongniart, from the Carboniferous coal deposits of Pennsylvania. *A*, a cast of the hollow interior of a small section of the stem (× $\frac{3}{4}$). *B*, a portion of the surface of this in detail. *C*, diagrammatic cross section of a mature calamite stem to show origin of the ribs and grooves upon the cast. *gr.*, grooves (internodal furrows) formed by the inwardly projecting ends of the vascular bundles; *i.ca.*, casts of infranodal canals opening in the medullary rays at the nodes; *m.r.*, medullary rays; *n*, nodes; *r*, ribs (internodal ridges) formed by the groove upon the inner surface of each medullary ray; *v.b.*, vascular bundles. (*A*, *B*, from Lesquereux.)

the equisetes were represented by forms which were probably intermediate between the Paleozoic and the living horsetails. Equisetites was a very large horsetail of the Triassic with a stem

eight inches in diameter and with over a hundred leaves in a whorl. Other fossil examples are:

1. **Calamites** (Figs. 25, 181), a tree often attaining a height of one hundred feet, usually preserved in the form of casts of the interior of the hollow stem. The markings on the surface of these casts are the print of the inner surface of the wood and do not correspond to the ribbing of the external surface of an Equisetum. These internal molds are marked with longitudinal ribs and furrows, and are jointed, as are the stems of the modern horsetails. The furrows are the imprints of groups of vascular bundles.

The stems branched and bore narrow, lance-shaped leaves arranged in whorls at the nodes, or joints, of the stem. A single nerve passed from end to end of the leaf. Certain cones described under various names when found separately have been found in connection with a few specimens of Calamites stems.

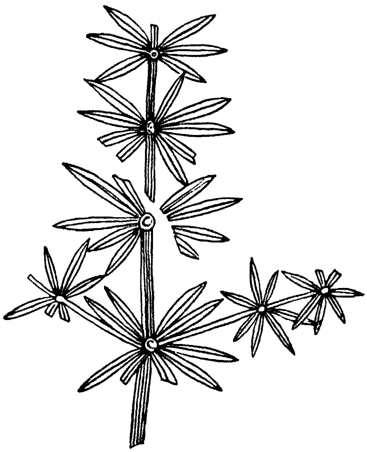


FIG. 26. — The ancient horsetail, *Annularia longifolia* Brongniart ($\times\frac{1}{2}$), from Pennsylvania, showing seven whorls of leaves. This flourished in the fresh-water coal swamps of eastern North America during the Pennsylvanian time. (Redrawn from Lesquereux.)

Calamites disappeared in the Permian; during the Pennsylvanian they were an abundant form in the coal swamps of eastern North America.

2. **Annularia** (Fig. 26), a smaller plant with a stem of two or three inches diameter, and abundant in the Pennsylvanian of eastern North America, is classed with Calamites as a near relative, if it is not actually in some cases merely smaller branches of that form. The leaves, as in Calamites, are quite large and they doubtless accomplished more photosynthesis than do the living horsetails.

1. What is the name of the only living genus of this order? Describe its appearance; its habitat.
2. How is photosynthesis carried on in the equisetes?
3. When in the past did this order include large forest trees? Name an example of such a tree.
4. Sketch Calamites: (1) two joints, surface view, (2) cross section. Label joint, leaf bases, position of vascular bundles.
5. Sketch Annularia; label leaflet. What is its probable relationship to Calamites? What is its age?

CLASS C. CLUB-MOSSES (LYCOPODIALES)

Living club-mosses are largely creeping, many-branched plants, with numerous tiny moss-like leaves, spirally arranged on the stem. The spore-bearing leaves are arranged in club-like cones as in the horsetails.

They embrace but four living genera, of which the two more common are Lycopodium and Selaginella. These two genera include nearly six hundred species, most of which grow in moist tropical forests. The common club-mosses of the temperate regions of North America and Eurasia belong to Lycopodium (Fig. 27). The living species are, however, merely a few decadent survivors of a very prolific class of the middle and late Paleozoic. They attained their greatest size and abundance in the Carboniferous, when they included many of the largest forest trees. In some of these a secondary growth took place through the activity of the cambium, much as in present-day gymnosperms and dicotyledons. The structure of their leaves and stems was also much more complicated than in the case of the living species of club-mosses. Since the Paleozoic this class has gradually declined *pari passu* with the increasing importance of the more specialized seed plants. Club-mosses are known from the Devonian to the present.

Derivation of name. — Lycopodiales (Greek *lukos*, wolf, + *pous* (pod), foot). The significance is not obvious, possibly from the prostrate, creeping stem. The common name club-moss is due to the moss-like stalks bearing club-like cones.

Lepidodendron (Figs. 28, 181). — This was a lofty tree of the later Paleozoic, appearing in the Lower Devonian and dying out in the Permian; it was especially abundant throughout the world during the Carboniferous.

The trunks were straight and somewhat palm-like, attaining at times a height of one hundred feet, and bore toward the top a crown of branches. Both branches and stems always forked dichotomously. The stems were densely clothed in long, simple, pointed leaves, much like those of the pine, which sometimes reached a length of six or seven inches. When these leaves were shed, their bases remained attached to the stem, thus covering the bark of the branches and even of the larger trunks with a distinctive spirally arranged ornamentation. Each of these marks of the former attachment of the leaves is rhombic in outline and somewhat convex. It is called a "leaf-cushion." The apex of its convexity represents the scar left by the fall of the leaf, while the remainder of the rhombic area is formed by the decurrent base of the leaf which has remained on the stem. The various marks upon the leaf-cushion

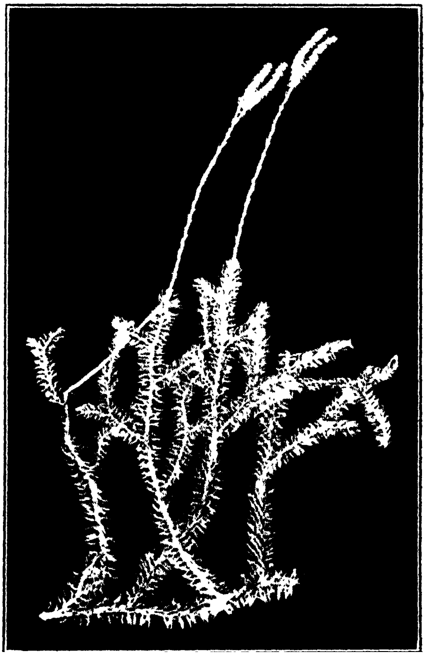


FIG. 27. — *Lycopodium clavatum* Linné (× $\frac{3}{8}$). A very common club-moss of North America and Eurasia. Also known as running pine and ground pine. Note the clubs at the tips of two of the pinnately branched aerial stems, rising from the creeping main stem.

are the prints of various parts of the stem of the leaf. Thus the central of the three dots on the lower edge of the scar itself is the severed end of the vascular bundle which formerly passed

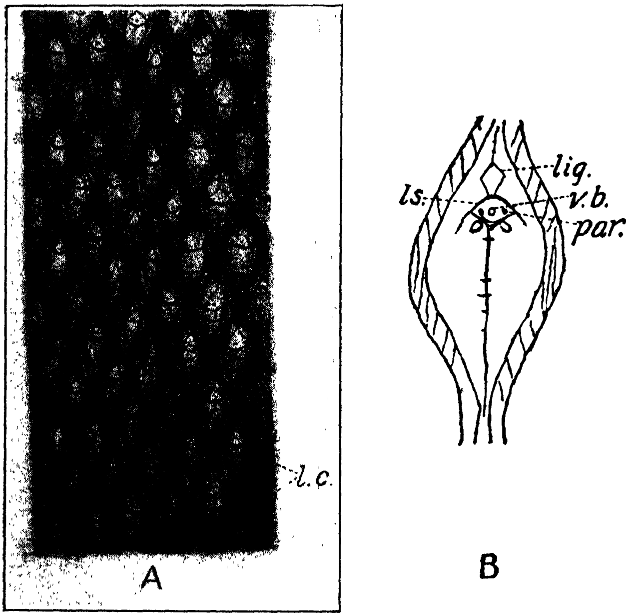


FIG. 28. — The ancient club-moss, *Lepidodendron modulatum* Lesquereux, from the coal horizon of Pennsylvania; Pennsylvanian in age. *A*, surface characters of a small part of a trunk (× ⅕). *B*, a single leaf-cushion; natural size. *l.c.*, leaf-cushion, — the entire rhombic area except the leaf scar (*l.s.*) and the base of the ligule (*lig.*); *l.s.*, scar left by the fall of the leaf; *lig.*, ligule; *par.*, lateral strands of leaf tissue (the parichnos), supposedly here respiratory in function; *v.b.*, vascular bundles, the main tubes for the transfer of sap to leaf and manufactured material back to trunk. (*A* from Lesquereux.)

out through the stem into the leaf, the other two representing strands of leaf tissue. The small triangular dot above the scar has been shown to mark the position of the ligule, a leaf-like organ present in Selaginella and Isoetes, living allies of Lepidodendron.

Our knowledge of Lepidodendron is based upon fossilized remains of all of its parts. The large trunks have been found abundantly in England in such a good state of preservation that the cellular structure is easily observed, while the peculiar ornamentation of the surface of the stem is shown by the external molds. In the great majority of specimens the leaf bases only are preserved; but attached leaves have been found in some of the calcified or silicified specimens of "coal balls," in which whole masses of stems, leaves, and fruits are found in a wonderfully preserved condition. These rather rare coal balls are simply concretions of silica, or lime, which formed around certain masses of the peaty vegetation as centers and, through inclosing and interpenetrating them, preserved them from the peculiar processes of decay which converted the rest of the vegetation into coal. In them the mineral matter slowly replaced the vegetable matter, molecule by molecule, thus preserving the cellular structure to a remarkable degree. Such balls are especially frequent in the coal of certain parts of England (Lancashire and Yorkshire).

Enormous spreading root-like underground stems occur in the rocks of the Pennsylvanian, apparently in the position in which they grew. Such root-like organs, to which the name **Stigmaria** has been given, were possessed by both Lepidodendron and the allied genus, Sigillaria. That they are not true roots is evidenced by their anatomical structure and their habit of branching, always into two, as has been noted in the stems of Lepidodendron. They bear many small appendages which seem to be true roots. Such root-bearing underground stems are characteristic of living lycopods; they were adapted for growth in wet ground where long roots were not needed for penetrating far into the soil for moisture.

It is in the fossil cones, showing its manner of fruiting, that Lepidodendron betrays its relationship to the living club-mosses. The cones of both fossil and living lycopods consist of scales arranged around an axis, each bearing on its upper side a large spore case containing many spores, all of one kind. These cones

of Lepidodendron are known by the collective name of **Lepidostrobus,** and usually occur as impressions in coal; the internal structure is well known from the study of the calcified specimens of the coal balls, together with several silicified specimens and casts. The cones vary from an inch to one and a half feet in length.

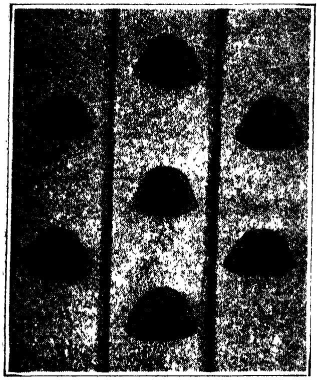


Fig. 29. — *Sigillaria polita* Lesquereux, from the Pennsylvanian formations of Pennsylvania, showing the leaf scars arranged in vertical rows. Natural size. (From Lesquereux.)

Sigillaria (Figs. 29, 181). — This was a tree which probably resembled Lepidodendron in general appearance as well as in geologic range. It differed in the structure of its stem and in the arrangement of leaves, as is indicated by the impressions of the bark covered with leaf-cushions. The leaf-cushions are hexagonal in outline and arranged in quite regular vertical rows. Its cones are known as **Sigillariostrobus.**

Its underground stems were discussed under Lepidodendron.

1. Name two common living club-mosses. Where have you seen them growing?
2. What is the geologic range of this class?
3. Sketch a leaf-cushion of Lepidodendron; label, where present, scar left by fall of leaf, the decurrent base of leaf, and of vascular bundle passing into leaf.
4. Sketch (reduce in size) a foot length of Stigmaria, a small portion in detail, indicating the little "roots." What was the function of Stigmaria?
5. Sketch a small portion of Sigillaria. How does it differ from Lepidodendron?
6. What are coal balls? Why are they important to the paleobotanist?
7. Why are the fruit, stem, and roots of Lepidodendron and Sigillaria known under separate names?
8. How do fossil lycopods resemble living ones?

CLASS D. SPHENOPHYLLALES

These are a Paleozoic group of slender plants with jointed stems, and leaves in whorls. They were probably trailing or climbing in habit, and are known from the Devonian to the Permian.

Sphenophyllum and a related Mississippian genus, Cheirostrobus, based on one of the most beautifully preserved fossil fruits ever recovered, combine to such a degree the characters of both the lycopods and the equisetes that the Sphenophyllales are held to be the descendants of the ancient stock from which club-mosses and horsetails have diverged in the course of evolution. The group became extinct at the close of the Carboniferous.

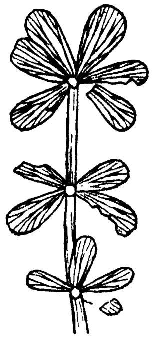


FIG. 30. — *Sphenophyllum schlotheimii* Brongniart, from the Pennsylvanian coal deposits of Pennsylvania. Natural size. (Redrawn from Lesquereux.)

Sphenophyllum (Fig. 30). — A small, branching plant with slender, ribbed stems, represented by many species in the Pennsylvanian coal fields of eastern North America. Leaves are usually six in a whorl and wedge-shaped or cut into lobes. Thus externally the plant resembles a small Calamites, but the anatomy of the stem and of the cone shows it to be different. The name, from the Greek *sphenos*, a wedge, + *phyllon*, a leaf, refers to the usual shape of the leaves.

1. Has this order any living representatives?
2. Describe Sphenophyllum.
3. How is this order related to the club-mosses and the horsetails?

CHAPTER V

PHYLUM IV. SPERMATOPHYTA

These include the most highly organized plants and are distinguished by the production of seeds (whence the common name of seed-plants). The difference between these and the lower groups is not, however, so great as at first appears. There is the same alternation of the vegetative (asexual) and reproductive (sexual) generations, the sporophyte and the gametophyte, as is seen in the Pteridophyta, but the alternation is less evident. Inequality between sporophyte and gametophyte is still more pronounced than in the fern.

The two chief distinguishing characteristics of the spermatophytes which sharply differentiate them from all other plants are: (1) the formation of a pollen tube (short in the gymnosperms, since the pollen grain is lodged within the ovule; long in the angiosperms), and (2) the production of seeds. The "seed" is the beginning of the sporophyte stage; the embryo within it later unfolds into the mature plant. In specialized organs within the flower or cone upon this plant there are developed the sporangia, either male or female. The female sporangium is called the ovule, and the male the anther sac. From these sporangia are discharged the spores — the pollen from the anther sacs, a specially differentiated cell from the ovule; these spores develop either into the male or the female gametophyte as the case may be, and from the union of their products results the fertilized ovum — the seed. All this process of formation of the gametophyte takes place within the flower.

In seed plants fertilization is not conditioned by the presence of water for the male gametophyte (shed microspore or pollen grain) carried by wind or insects to the vicinity of the mega-

spore, develops a tube (pollen tube) down which the male gametes are carried by the flow of protoplasm to the female gametophyte. (Cilia by means of which in the lower plants the male gamete swims to the female are lacking in all except the most primitive of the seed plants.) The megaspore is never released from the megasporangium (ovule), but, together with the female gametophyte, the embryo sporophyte, the megasporangium wall, and sometimes a mass of nutritive tissue (endosperm), becomes the seed.

For discussion of the procedure of fertilization see page 103.

Derivation of name. — Greek *sperma*, seed + *phyton*, plant. The members of this division are distinguished by the production of seeds.

The spermatophytes are divided into the classes:

CLASS A. GYMNOSPERMS (GYMNOSPERMÆ)

These plants may be typified by the pines. In the female pine cone each scale is a leaf that is a megasporophyll (known also as a pistil or carpel); upon the base of this two ovules develop; the surface of each of these becomes very hard and is often extended to form a wing which catches the wind and carries it some distance from the parent tree. The megasporophyll does not inclose the ovules.

Derivation of name. — Gymnosperm > Greek *gymnos*, naked + *sperma*, seed. The seeds are not covered by the megasporophyll.

These are trees and shrubs, mostly evergreens. They include the following orders:

a. Cycadofilicales
b. Cycadales:
  1. Cycadeoideæ
  2. Cycadeæ
c. Cordaitales
d. Ginkgoales
e. Coniferales
f. Gnetales.

Order *a*. Cycadofilicales (Seed Ferns)

A Paleozoic group of plants with fern-like leaves (Fig. 181). They were often fern-like in habit, though including likewise vines and trees. They were formerly thought to be ferns because of the form and venation of their leaves. No sporangia, however, were found on any of the leaves and hence it came to be suspected that they might not be true ferns. Stems were finally found in association with some of these leaves whose anatomy combined characters of ferns and cycads. Later true seeds were found attached to stalks bearing the fern-like leaflets. These plants were accordingly shown to be primitive seed-plants intermediate between the ferns and the cycads, a relationship indicated by the name applied to them. In some the cycad features predominate, in others those of the ferns.

Of those fruits which may belong to this gymnospermous line, one of the most important yet discovered is that shown in the adjoining Figure 31. It accompanies cycadofilicalean foliage in some abundance in the ironstone nodules of Mazon Creek, Illinois, and in its outer features closely resembles the fruits described in England as the seeds of Neuropteris. The full meaning of this ancient type of fructification is not yet understood. If, as is quite possible, it is the male flower of Neuropteris, there was a very strong resemblance between the male and female flowers of some of the cycadofilicaleans. This would seem to indicate that their immediate ancestors were heterosporous ferns which gradually developed the seed habit, the sporangia gradually enlarging into true seeds.

During the change from homospory to heterospory and from that to the seed condition, the leaf and stem remained practically unchanged. It is thus very easy to mistake the early seed plants for ferns. That this was the line of evolution seems to be indicated by the ontogeny of the living heterosporous ferns. And as the megaspores became larger, development would proceed farther before the spores were shed, until, finally, the megaspores would not fall out of the sporangium. Then, by defini-

tion, the sporangium with its contained megaspore would be a seed and the plant would belong to the gymnosperms.

It has been estimated that the Cycadofilicales formed fully half of the known vegetation of the Carboniferous coal deposits.

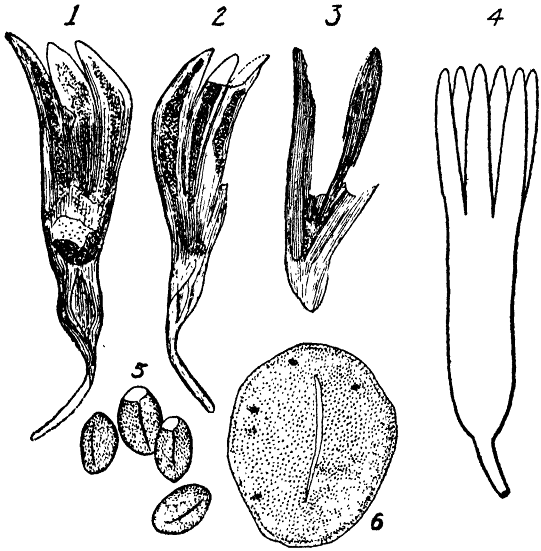


FIG. 31. — Codonotheca, one of the most singular and ancient microspore-bearing fruits known. From the Pennsylvanian of Mazon Creek, Illinois. *1–3* show the interior faces of the lobes covered with spores just as brought to view when the nodules in which the fruits are embedded are split open. *5–6* are the spores enlarged 28 and 85 times respectively, while *4* is a restoration of the flower-like fruit, natural size. (From Sellards.)

Neuropteris (Fig. 32). — This is an example of one of the most familiar of the fern-like fronds of the Pennsylvanian coal deposits. The leaves are very large and compound, being bi-, tri-, or quadri-pinnate, with oblong leaflets which are usually attached to their common stalk by a short stem. Each bears a median nerve from which spring secondary ones. The leaves therefore are fully fern-like in superficial appearance. That Neuropteris was not, however, a true fern was suspected from

the constant absence of sporangia from the leaves and this conclusion was established by the finding of leaves of the Neuropteris type in association with cycad-like stems bearing true seeds.

Pinnules of this genus are abundant in the Mazon Creek iron carbonate clay concretions. These Pennsylvanian strata in Grundy County, Illinois, have in this manner preserved with-

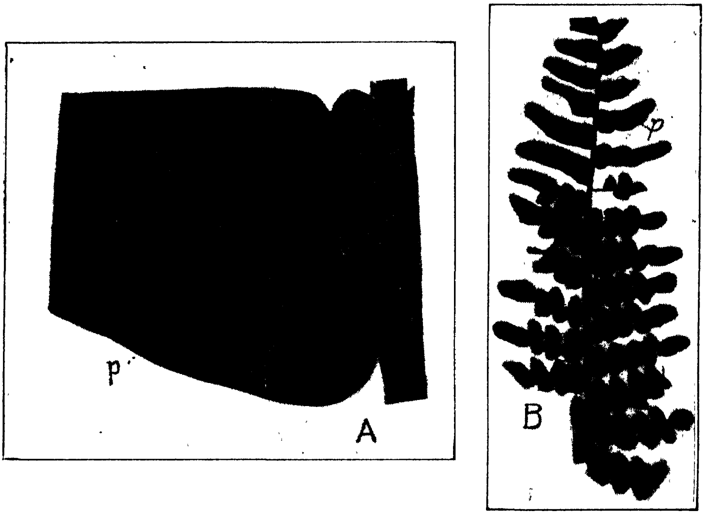


FIG. 32. — Examples of the cycadofilicales (an extinct class combining characters which to-day are separated into the distinct groups of ferns and cycads). *A*, *Neuropteris hirsuta* Lesquereux; a portion of two leaflets (pinnules, *p*), with the small stipules (*s*) at their base. *B*, an almost complete frond of *N. smithsii* Lx. Both (natural size) from the Pennsylvanian period of Pennsylvania. (From Lesquereux).

out crushing and in wonderful perfection not only plant remains such as Neuropteris, Pecopteris, and fruits, but also crustaceans, insects, and fish-bones.

Pecopteris. — Fronds much like those of Neuropteris, and of similar age, but leaflets attached to the stalk by their whole width and touching one another. The small, flat-winged seeds are well known in *P. plunckneti*. (See Fig. 8.)

Lyginodendron. — Stems varying in diameter from one-eighth of an inch (3 mm.) up to an inch and a half (4 cm.), not branching, but very long, bearing many leaves. Leaves very large, much divided, and fern-like in appearance.

That Lyginodendron was a climbing plant is considered likely from the slenderness of its stem in proportion to its length and from the presence of spines on stems and leaves.

Fragments of the stems and leaves of this plant occur very abundantly and in well-preserved condition in the calcareous nodules or coal balls of the English Carboniferous coal deposits mentioned above.

The plant has very nearly the stem structure of a cycad, but a fern-like leaf. Highly organized seeds have been found in a definite connection with this leaf, which shows that Lyginodendron, instead of being a fern as was formerly supposed, was a seed-plant. It was still, however, a very primitive seed-plant, for both seeds and pollen sacs were borne on slightly altered portions of the ordinary leaf. Lyginodendron is thus seen to be a noteworthy example of synthetic types, that is, of forms that combine characters which afterward separate and distinguish separate orders.

1. What are the two chief distinguishing characteristics of the Spermatophyta?
2. Describe the formation of the sporophyte and the gametophyte stages in the spermatophytes.
3. Into what classes are the spermatophytes divided?
4. What is the difference between a gymnosperm and an angiosperm? Show that this difference is indicated in the derivation of the name. Name three common living gymnosperms.
5. Into what orders are the gymnosperms divided?
6. What are the Cycadofilicales? In what respect do they resemble ferns? How are they like cycads? When were they most abundant? Name an example.
7. Sketch a Neuropteris pinnule. How is it known that this is not a fern?
8. For what is Mazon Creek famous?
9. In what respect is Lyginodendron a synthetic type?

Order *b*. Cycadales

Family 1. CYCADEOIDEÆ. — This extinct family of trees or shrubs resembled the living cycads in general outer appearance.

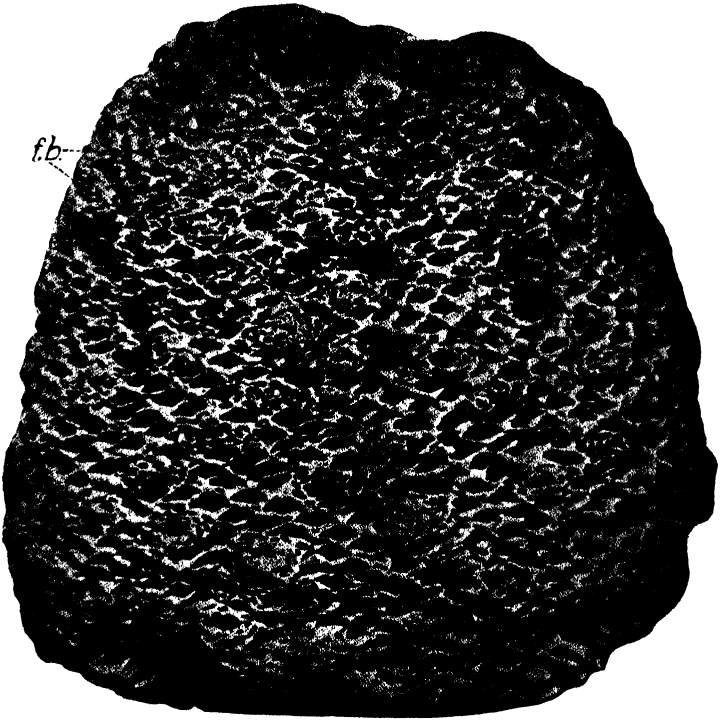


FIG. 33. — A fossil cycad, *Cycadeoidea marylandica* Fontaine (× ¼), from the Potomac formation (Lower Cretaceous) of Maryland. At the time of fossilization it was about to blossom. Nearly thirty flower buds (*f.b.*) show here between the old leaf-bases. The wonderful preservation of some of the flower buds embedded in these ancient fossilized trunks is seen in Figure 35.

The stem in most forms was thick and short and closely covered with an armor of persistent leaf-bases (Fig. 33). Among these leaf-bases were wedged numerous small branches, each

terminating in a fructification. The stem usually bore at top a crown of large Cycas-like leaves (Fig. 34).

As in general appearance, so likewise in the anatomy of the stem, there was a close similarity between these plants and the living cycads. Some of their characters, such as their lateral branching and the hairlike and papery scales profusely covering the leaf-bases, recall the cycadofilicales and the ferns. In the structure of their fruiting organs, however, the cycadeoids were peculiar to themselves, and showed an advance over the other orders. They had a true flower since both male and female organs were borne on the same axis and were arranged in the manner typical of the later flowering plants — the angiosperms. This flower (Figs. 35, 36, 37) consisted of a sheath of hairy overlapping bracts inclosing a circle of leaf-like, pollen-bearing organs analogous to stamens, central to which is a conical axis bearing stalked seeds, the "receptacle" of higher plants.



FIG. 34. — *Cycadeoidea jenneyana.* Photograph (× 3) of a longitudinal section through a silicified young leaf not yet emerged from the bud. (From Wieland.)

The seeds are often so well preserved in various species that the embryo may be distinguished; this is dicotyledonous, differing from that of other gymnosperms in occupying nearly the whole seed. This is, however, the only order of fossil plants in which an embryo has been sufficiently well preserved to be studied in detail.

In general appearance, therefore, these plants at once suggest the cycads; in the large, leaf-like stamens and certain features

of their pollen sacs they indicate an affinity with the ferns, and in the possession of true flowers they distinctly approach the angiosperms.

It has seemed evident to students of these analogies that the cycadeoids, as their name implies, are closely related to the

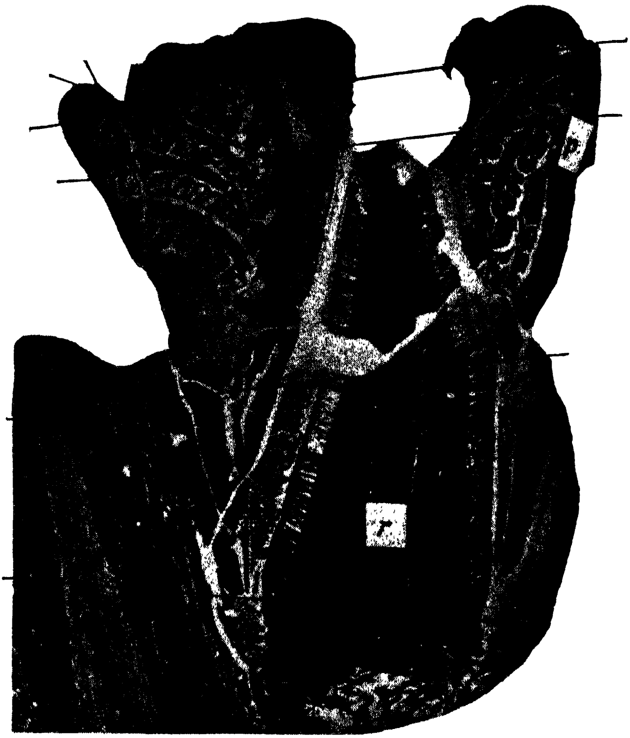


FIG. 35. — The unexpanded flower of *Cycadeoidea dacotensis* Macbride, from the terrestrial deposits of Upper Jurassic age in South Dakota. Photograph (× 2) of a vertical section of a silicified specimen. The lines refer to various sections through the flower published in Wieland's "American Fossil Cycads." *p*, pinnules: *r*, receptacle.

cycads, and that both groups sprang separately from certain Paleozoic ferns, the marattiaceous type. Moreover, the structure of their fructification, the arrangement of its parts into a

"flower," suggests that the cycadeoids represent an intermediate stage in the supposed line of development of the angiosperms from their fern ancestors.

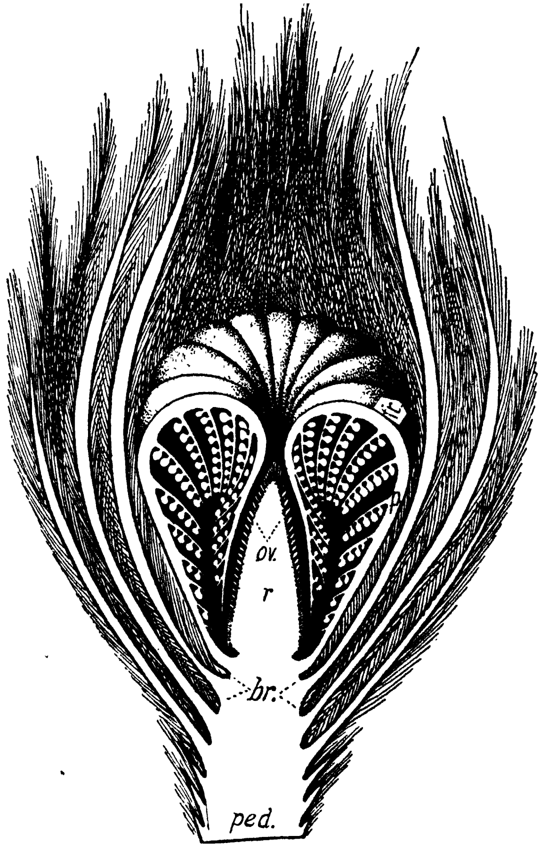


Fig. 36. — Restoration of flower bud of Figure 35, based upon many other examples besides this figure. Nine of the eighteen staminate fronds (*fr.*) are shown folded with reduced pinnules (*p*) bearing densely packed oval synangia, — pollen sacs (in white). At the center is the pistillate portion of the flower, the elongate conical receptacle (*r*) covered externally with short stalked ovules (*ov.*) separated by scales. *br.*, bracts; *ped.*, pedicel, or stalk, attaching the flower to the stalk. (Both figures from Wieland.)

This order formed the dominant vegetation of the Mesozoic ranging from the Triassic into the Potomac Lower Cretaceous. It was exceedingly abundant during the Jurassic in North America, Europe, India, and the Arctic regions. Especially fine representatives of the genus Cycadeoidea (Bennettites) are found in the upper Mesozoic of Maryland, South Dakota, Wyoming, and Mexico. The genus Wielandiella from the Upper Triassic (Rhætic) had slender stems branching dichotomously and bore its flowers in the forks. Another genus, Williamsonia, is also of varied structure and had a cosmopolitan distribution in the Jura-Cretaceous.

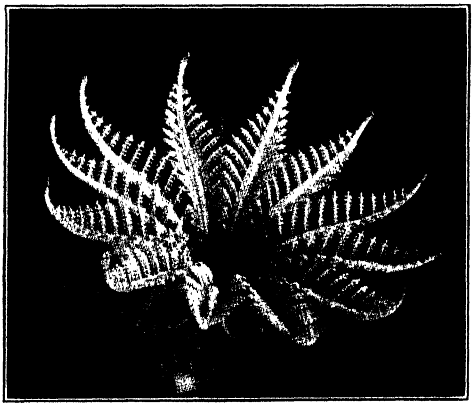


FIG. 37. — Restoration of an expanded cycadeoid flower. The central seed-bearing cone is surrounded by stamens, each of which has the form of a pinnate fern frond. The stamens are bordered without by sterile bracts. (View of a glass model by Dahlgren from the Field Museum, Chicago; based upon dissections by Wieland.)

Family 2. CYCADEÆ, the existing cycads or sago palms. — Plants with thick, columnar stems, at times attaining a height of thirty to sixty feet. The trunks are covered with an armor of old leaf-bases and bear a crown of large, usually once pinnate leaves, with from one or two apical cones to as many as thirty in one Australian form. The fructifications are in nearly all genera cones, either male or female, the sexes being separate on different plants. In the female plant of the living Cycas, however, the reproductive organs are not compacted into a cone, but consist of simple, leaf-like blades on which are borne the unprotected seeds. This is the simplest arrangement of repro-

ductive organs among living seed plants and is reminiscent of ferns.

Another primitive character of the cycads is their method of fertilization. In most of the living seed plants the male cells are carried by the pollen tube to the ovule (Fig. 23, *E′*). In the cycads and ginkgos alone among seed plants the male cells are ciliated and motile, swimming actively to the ovule after the rupture of the pollen tube, as is usually the case in the cryptogams — the ferns, mosses, and many algæ. This motility of the male cell is a survival of the earlier stages of the process of plant evolution when water was an essential medium for the process of fertilization, and of a still earlier stage when the whole plant body was adapted to life in the water.

Living cycads are tropical. There are nine genera, of which Cycas, the best known eastern genus, is found in Asia and Australia, and Zamia is the most conspicuous American genus. They existed in the Mesozoic in some number, but so far definite evidence of them remains meager; it is the abundance of their kindred, the Cycadeoideæ, that marks out the Mesozoic as the " Age of Cycads," or as some name it " the Age of Proangiosperms." The genus Cycas has been found in the Lower Jurassic, though its leaf type goes back much farther.

1. Into what two families are the cycads divided? Describe each briefly, stating one respect in which they resemble each other; one in which they differ. What is their geologic range?
2. Where are cycads living at present?
3. Why is the motility of the male cell especially interesting?
4. Among what plants was the first flower evolved? Did it resemble any modern flowers? What testimony does it furnish upon the origin of the higher flowering plants?
5. Sketch Cycadeoidea, labeling bracts, flower buds (if present).
6. What do the bracts represent?
7. Make restoration of the entire plant, naming the stem, crown of leaves.
8. What was the age of cycads?

Order *c*. Cordaitales

An extinct group of tall, slender trees which had a general distribution throughout the world from the Devonian to the Permian, inclusive. It is represented by the genus **Cordaites.** The trunk rose to a height of thirty to one hundred feet and was surmounted by a dense crown of branches bearing narrow swordlike leaves. The leaves were distinguished by their conspicuous parallel veins, and their great size, attaining at times a length of three feet.

The general structure of the stem resembles that of the conifers except in the very large pith, which suggests rather that of the cycads. Casts of this pith cavity, called **Sternbergia,** are common fossils. They are cylindrical bodies, one to four inches in diameter, longitudinally ribbed and marked by transverse constrictions at short intervals. The pith in the living stem ruptured transversely at intervals, dividing into disks of solid tissue separated by empty spaces. In the casts of this cavity, where there is a later decay of the pith and wood, the position of the pith-disks would be represented by transverse constrictions. This appearance may be seen on a lesser scale in the pith of the walnut, hickory, and other common trees to-day.

The fructifications of Cordaites were small male and female catkins.

In leaf structure and in certain primitive features of the seeds, Cordaites shows relationship to the Cycadofilicales, in stem and root anatomy it inclines toward the conifers (Fig. 38), while its male catkins resemble those of the Ginkgo. From these and other characters it is evident that the Cordaitales were a highly generalized group of seed-fern affinity near the base of all the later gymnosperm lines, originating probably in the Silurian. Among living gymnosperms, the ginkgos are their closest kin.

The Cordaitales are confined to the Paleozoic and seem to have furnished the predominant members of the gymnosperm

forests during the Devonian, and especially later during the Carboniferous.

Cordaites, named in honor of the early paleobotanist, Corda, is the best known genus. In the Upper Devonian black shale

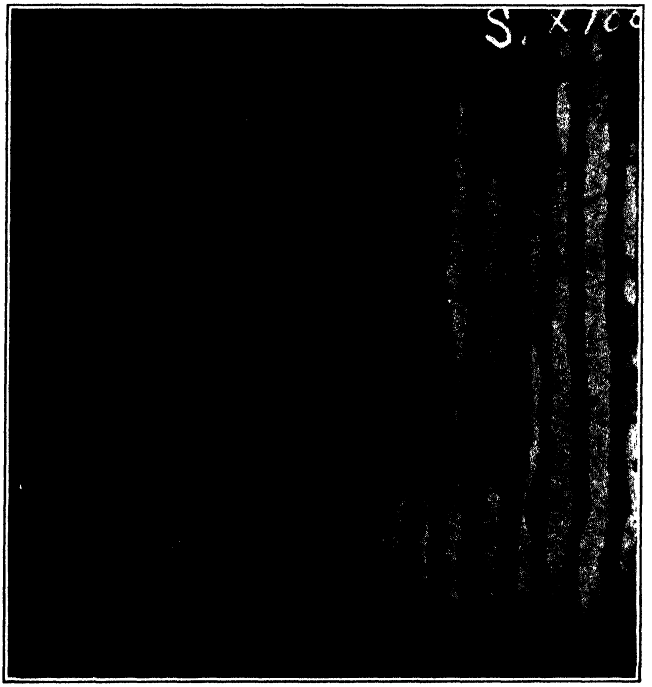


Fig. 38. — Photomicrograph of a radial section of one of the most ancient of known woods, *Callixylon* (*Cordaites*) *oweni* Wieland, from the Upper Devonian Black Shale of Indiana. The preservation of this wood is so perfect that the thin sections may be freely studied at 600 diameters. At the 100 diameters shown here, the bordered pits of the radial surfaces of the wood cells or tracheids are seen to have a radially grouped arrangement; this radial grouping is rare in the Paleozoic. (After Wieland.)

of Indiana are trunks two feet in diameter and twenty feet long, indicating trees probably one hundred to one hundred and fifty feet high (Fig. 38). In Pennsylvanian shales in

New Brunswick the leaves are packed in layers like those of modern forests.

1. Describe the appearance of Cordaites.
2. How were casts of its pith cavity formed? What are they called?
3. Discuss its relationships and probable evolution.
4. Describe a forest of Carboniferous time as you think it must have appeared.

Order *d*. Ginkgoales

An isolated order of gymnosperms, represented at present by only one genus and one species, *Ginkgo biloba*, the maidenhair tree, but with the long and varied ancient history that such isolation in the existing flora always indicates. The ginkgo is a tree which in general appearance and in the anatomy of the stem closely resembles the conifers. The leaves, however, are fan-like in outline like the large leaflets of the maidenhair fern, and are shed each year.

A primitive character which it possesses along with the cycads, and which is reminiscent of a fern ancestry, is the motility of the male cells in fertilization, already mentioned (p. 93).

The ginkgo tree has long been cultivated by the Chinese and Japanese, especially in the temple grounds; now a common cultivated tree, it is not surely known wild in any part of the world, though it may possibly be native to western China. It is the last member of a race that is seen by the fossil records to have spread over all the world. This race, the Ginkgoales, was especially numerous and widespread in the Jurassic and was still abundant in Cretaceous time. Leaves and flowers of representatives of this order are found in rocks of these ages in Europe, northern Siberia, Greenland, Spitzbergen, China, Turkestan, Australia, South Africa, and the Pacific Coast of America. In at least the earlier part of the Tertiary, the ginkgo flourished in Alaska, Greenland, and the northern part of Great Britain. Because of its great antiquity and isolated position it has been called a "living fossil." It is supposed to have arisen from the group of the Cordaitales.

1. Describe the ginkgo tree. What is its common name and from what derived?
2. What is the geologic range of this order?
3. Discuss the present and former geographic distribution of the ginkgo tree. Can you account for this difference?

Order *e*. Coniferales

This order includes the conspicuous gymnosperm vegetation of the north temperate regions, made up of trees and shrubs, mostly evergreen, usually with rigid, needle- or scale-like leaves and with male and female cones. The conifers were probably derived from the Cordaitales of the Paleozoic, retaining fewer primitive characters than the Ginkgoales, but derived from the same source. Living conifers are represented by about forty genera and three hundred and fifty species. They are divided into two families:

1. **Taxaceæ, the yews.** — With fleshy seeds and exposed ovules. Comparatively modern, with no record below the Lower Cretaceous, they already during this period formed an important element in the Potomac flora of eastern North America.

2. **Pinaceæ.** — With dry seeds and ovules covered by scales. These include four tribes:

(*a*) *Araucariæ.* — A group that is now mainly restricted to a small region of the southern hemisphere — Norfolk Island, Brazil, southwestern Argentina, and Chile, but widely distributed during the Mesozoic, being abundant in the Jurassic rocks of Great Britain, Spitzbergen, South Africa, Australia, India, the eastern United States, and in the Antarctic regions. A comparison of the former and the present distribution of such a family is of vivid interest as indicating former geographic connections which are now severed.

A fossil form of this group which is exceedingly common in the Petrified Forest at Adamana in eastern Arizona, is *Araucarioxylon arizonicum.* Into this locality many thousands of trees were washed down from the Triassic highlands to the west and, inclosed in the coarse sands and gravels, became

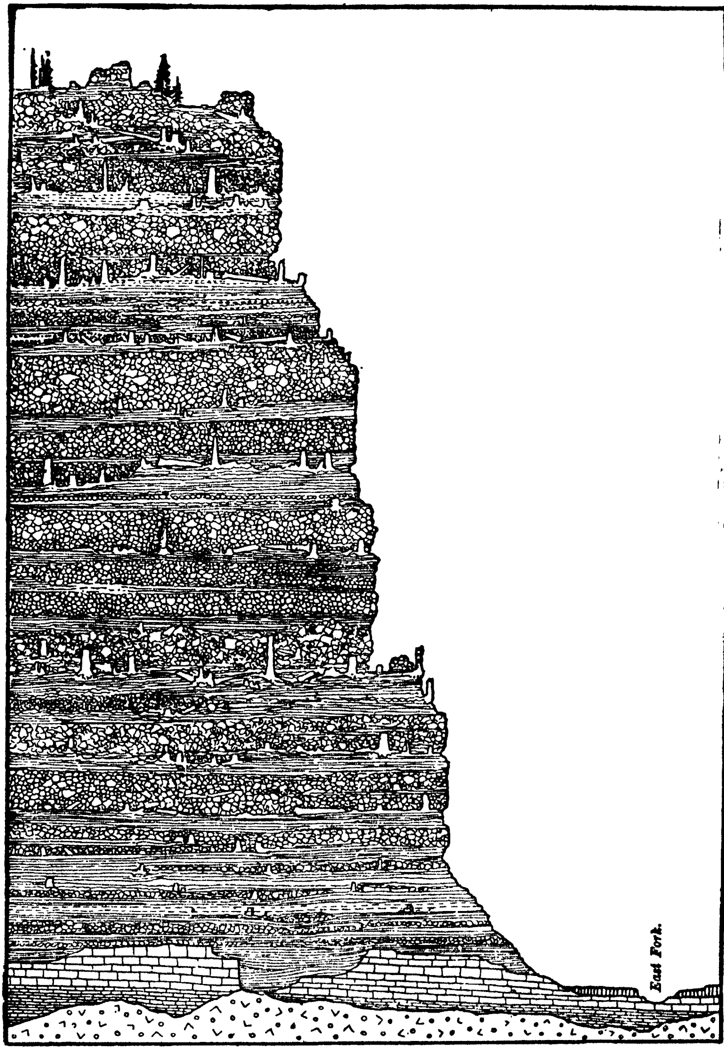


FIG. 39. — An ideal section through the fossil forests of Amethyst Mountain, in the Yellowstone National Park. There occur in this region 2000 feet of volcanic material in layers alternating with at least fifteen successive forests, indicating thus fifteen volcanic outbursts separated by at least sufficient time to allow the growth of forest trees (Sequoia, etc.) with a diameter of two to ten feet. (From Holmes.)

gradually silicified (Fig. 5). A fine araucarian forest of Triassic age also is in Patagonia, Lat. 48° S. Here, inclosed in sandy volcanic ash, are trees, branches, and cones, beautifully petrified, many of the trees being in their place of growth.

From the association of fragments of petrified araucarian wood with the jet at Whitby, England, it may be supposed that

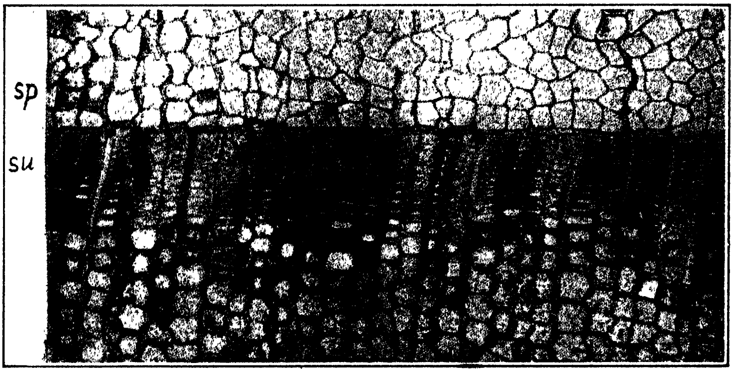


Fig. 40. — Transverse section (× 60) through an annual ring of the Tertiary conifer, *Sequoia magnifica* Knowlton. *sp.*, cells added during spring or wet season when an abundance of moisture caused rapid growth, hence large cells; *su.*, cells added during summer or dry season; the cells here are small. The change is gradual from the moist spring to the succeeding dry season, but the next spring's growth begins suddenly, hence here is a very sharp change in size of cells. These more or less sudden changes produce the annual ring, merely a contrast in size of cells, contrasting periods of slow and rapid growth. (From Knowlton.)

some of the jet, at least, consists of the fossilized remains of the wood of Araucaria.

(*b*) *Abietæ.* — The group of the more common evergreens — pines, cedars, hemlocks, etc. Recorded from the time of the Lower Cretaceous.

(*c*) *Taxodiæ.* — Includes (1) Voltzia from the Upper Permian and Triassic. To this tribe likewise belongs (2) Sequoia (Figs. 39, 40). The genus Sequoia is now represented only by two species — *S. sempervirens*, the redwood, and *S. gigantea*, the big tree — living in restricted areas in California and

southern Oregon. These trees are unique in the world in their size, age, and scarcity. The trunk often attains a height of over three hundred feet and a diameter of over thirty feet. Like Araucaria, Ginkgo, etc., Sequoia, as at present represented, is merely the lonely survivor of a once widely distributed group.

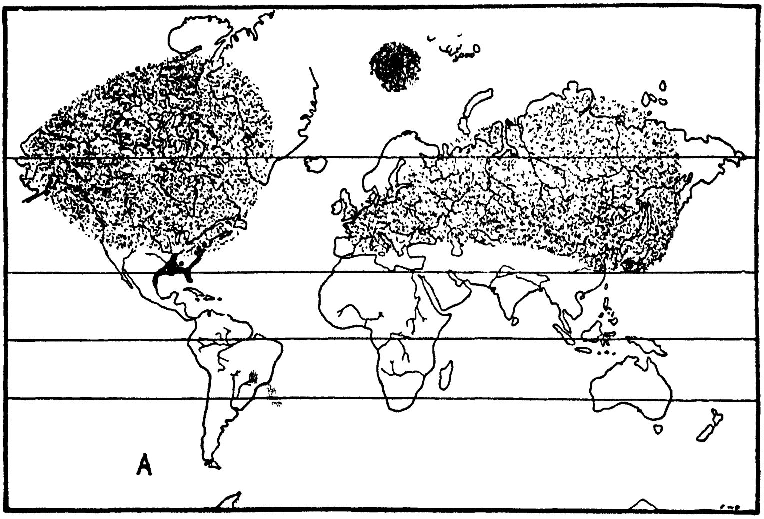


FIG. 41, *A*. — Sketch map showing the known distribution of the bald cypress (Taxodium). Tertiary distribution shaded; Pleistocene occurrences north of its present limits, in dots; present distribution black. (From Berry.)

Though not known conclusively from the Jurassic, its twigs, cones, and seeds are abundant in the Lower Cretaceous of North America from Virginia-Texas-California, north to Greenland, in Spitzbergen and Europe from Russia to Portugal; it continued in abundance and with wide distribution during the Cretaceous and Tertiary, but disappeared during the cold climate of the Pleistocene, except in the California-Oregon region. *Sequoia langsdorfii*, the direct ancestor of the redwood, was very widespread in the great circumpolar conifer forests of Upper Cretaceous time; while *S. magnifica*, so abundant in the

Tertiary of the Yellowstone National Park, was almost identical with the living redwood. (3) The genus Taxodium (Fig. 41, *B*, consisting of the bald cypress, characteristic of hard or sandy bottom swamps, and of a Mexican species, is now confined solely to the southern Atlantic and Gulf Coastal plain; but in early Tertiary time this genus was as Figure 41, *A*, shows, universal north of the tropic of Cancer. Such a map indicates the tremendous changes in plant distribution brought on by the advent of glacial conditions in the north polar area, while the recent description of the fossil flora of Graham Land (Upper Jurassic) by Halle shows like changes on a gigantic scale in Antarctica.

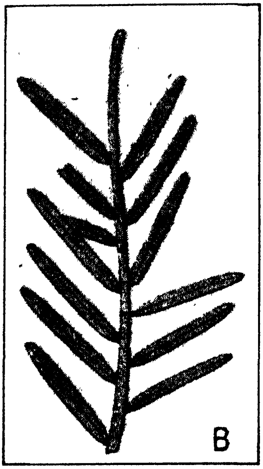


FIG. 41, *B*. — A twig of *Taxodium distichum miocenicum* Heer (× 2), from the Tertiary of Utah. (From Lesquereux.)

(*d*) *Cupresseæ*. — Including the juniper, arbor vitæ, etc. Known doubtfully from the Jurassic.

1. Name three living conifers with which you are acquainted.
2. What is the geologic range of this order?
3. Into what two families is it divided?
4. Describe the origin of the petrified trees at Adamana. What is their age?
5. What is jet?
6. Discuss Sequoia, noting its appearance, present habitat, and former distribution.
7. How did the climate of the Tertiary differ from that of the Pleistocene and the present? What was the chief cause of this difference? Give examples among plants that show that this climatic change took place.

Order *f*. Gnetales

This group of small trees or shrubs consists of three living genera, including Ephedra of the desert regions of both hemispheres. They differ from other gymnosperms and show some-

what angiospermous tendencies in certain structural characters of the wood and in some flower-like features of the reproductive organs.

Fossil record of the order would have high interest but so far has not been forthcoming.

1. What are the Gnetales?
2. What fossil record have they?

CLASS B. ANGIOSPERMÆ

As the mammals represent the culmination of the much-branched animal line of ascent, so the angiosperms contain the plants of highest rank. This group, the latest to come upon the earth, comprises over half of all known living species of plants. It is the angiosperms which clothe most of the earth with vegetation; in every climate and at almost all altitudes they nearly always compete successfully with all other vegetal types. They not only cover much of the earth with forests and grasses, flowering herbs and shrubs, but many species (*e.g.*, water-lily, duckweed) have invaded the fresh-water realm of the algæ with wonderful success. Though very few angiosperms, as the eel-grass (Zostera), have tried to dispute with algæ a habitat in the sea, they are the only group to have invaded the sea at all, for the gymnosperms, ferns, and mosses have no representatives there.

The members of the angiosperms are commonly known as the Flowering Plants (Fig. 42). The typical flower is composed of (1) a covering, the *perianth*, which may consist of an outer bud-covering portion, the *calyx*, and an inner colored portion, the *corolla*. The entire perianth may be brightly colored or uncolored. Within the perianth are (2) the male organs — the *stamens* bearing the pollen, which are the male cells of fertilization. The stamens are arranged in one or more circles; at their center is (3) the female organ, the *pistil*, the outer portion of which, the *stigma*, receives the pollen while the inner portion,

the closed *ovary*, contains the ovules which after fertilization by the pollen become *seeds*.

Each part of the flower is a specially modified leaf. In the white water-lily, for example, the change from the green calyx to the white corolla and on to the pollen-bearing stamens is readily seen. The pistil, corresponding to the scale of a pine cone, is, like it, a megasporophyll. In the legumes (peas and beans) the split pod (ovary or megasporophyll) shows well its

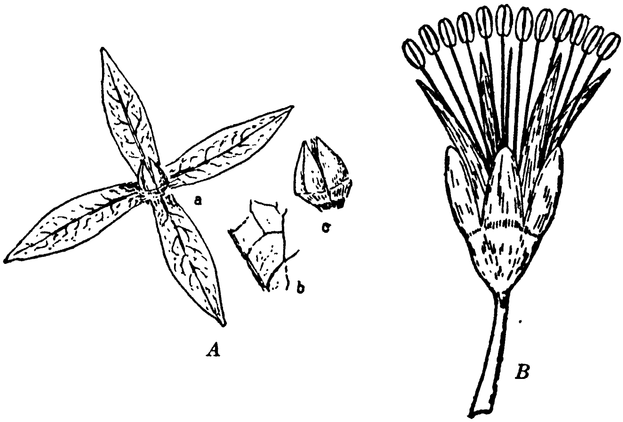


FIG. 42. — Fossil flowers, because of their delicacy, are rarely preserved. *A*, *Carpolithes macrophyllus*, from the Miocene shales of Florissant, Colorado. (From Cockerell.) *a*, entire flower with its four large calyx lobes; *b*, detail of venation; *c*, fruit. *B*, restoration of flower of *Combretanthites eocenica*, from the Eocene of Tennessee. × 4. (From Berry.)

leaf-like origin and also its protection of the seeds (peas) within. In the apple five pistils fuse to form one structure; within this are developed the seeds, while the edible fruit is the enlarged growth of the outside covering (the receptacle) of this compound ovary. In the cherry and peach the outer part of the ovary is the fleshy edible portion and the inner part is the hard stone (the true seed is within this).

The method of *fertilization* is somewhat complicated. Each dust-like pollen grain is a single cell with a single nucleus at its center. When this pollen grain is lodged, through the agency

of the wind or an insect, against the stigma, the usually sugary solution there holds it and causes it to grow. By this time the single nucleus will have divided into two or three parts, one of which, the tube cell, gives rise to the pollen tube, which piercing the stigma grows down its stalk and penetrates an ovule, permitting the passage thither of the other two cells (Fig. 23, *E'*). By this time the nucleus of the ovule has also divided several times, forming several cells; to one of these cells one of the two male cells is attracted, and there results a fusion of the two cells into one; this fusion is fertilization. Immediately this new cell, nourished by the other cells, grows rapidly into a minute embryo. This embryo consists of a stem with seedling leaves (cotyledons) at one end, and a root at the other. In this state, the *seed*, it ceases growing and may remain dormant for years. As animals prepare food material — the yolk — for the growing embryo, so also do plants; in the grasses and palms this nourishment lies in the seed outside the cotyledons, in the bean and walnut within the cotyledons themselves.

It is thus seen that the pollen grain and ovule always develop into distinct plants of a few cells each, usually three in the former and eight in the latter. These few cells form the sexual or gametophyte stage of the angiosperms, corresponding to the entire liverwort and moss plant and to the prothallus of ferns. The union of two cells, one from each of these plants, produces the embryo which under favorable conditions will develop into the adult plant — the asexual, or sporophyte stage; it, like the fern-plant or the little capsule of the moss, produces spores called here the pollen and ovules.

Both subclasses of the angiosperms made their first appearance, so far as known, in the upper part of the Lower Cretaceous. Here appeared such modern dicotyledonous genera as the poplar, willow, laurel, and fig, as well as primitive representatives of such monocotyledonous families as the pondweed and the sedge. This early flora is best known from the Upper Potomac formation (Patapsco) of Virginia and from strata of corresponding age in Portugal. Later upon the Cretaceous lands flourished

very luxuriantly many of our best known living plants — the oak, walnut, beech, birch, holly, and ivy of the dicotyledons, the lily and palm of the monocotyledons. The rapid rise of the angiosperms — the true flowering vegetation — was probably due to the *pari passu* development of flower-loving insects, the bees and wasps (Hymenoptera) and the butterflies and moths (Lepidoptera).

Derivation of name. — Angiospermæ > Greek *angeion*, a vessel + *sperma*, seed, because the seed is inclosed in a protecting megasporophyll, *e.g.*, the core of an apple, the chaff of grass.

The Angiospermæ are divided into the subclasses:

a. Monocotyledones

b. Dicotyledones.

SUBCLASS A. MONOCOTYLEDONES

These plants are usually distinguished by the following characters: the plant begins with a single leaflet or cotyledon (whence the name mono-cotyledon); the leaves are parallel-veined; the stem is cylindrical with the vascular bundles scattered, a cross section accordingly not showing concentric growth lines; the roots are fibrous; the parts of the flowers in threes.

This subclass includes to-day members of vast economic importance to man. The grasses, especially their fruit, the grains, have become an absolute necessity to him in the temperate zones, just as the plantain, banana, and various palms (*e.g.*, date, coco, and sago palms) are now an essential to his existence within the tropics. Representatives of the subclass are first known from the upper part of the Lower Cretaceous of eastern North America and Portugal in such lowly forms as the pondweed and sedge; the lily and palm, however, soon appeared in the Cretaceous, while not until rather late in the Tertiary did true grasses make their appearance.

The paleontologic record of the palms goes back to the mid-Cretaceous (Fig. 43). It is probable that they occurred rather

extensively from this time on; they were apparently abundant in North America, both on the coastal plain and in the formations of the continental interior.

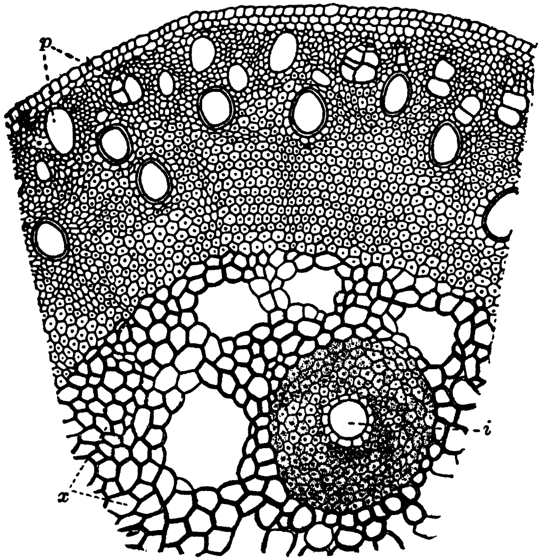


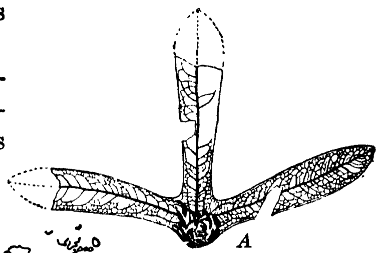
FIG. 43. — Transverse section of the New Jersey Upper Cretaceous palm, *Palmoxylon anchorus* Stevens. This is an example of the often marvelous perfection of preservation of cell structure in fossilized plants. Portion of a large root (× 130); *p*, phloem, thin-walled cells, through which most of the organic substances manufactured by the leaves pass down to the roots; *x*, xylem, thick-walled woody cells through which the crude materials absorbed from the soil pass up to the stem and leaves; *i*, an internal vessel surrounded by sclerenchyma fibers, — very thick-walled, strengthening cells. (After Stevens.)

SUBCLASS B. DICOTYLEDONES

The dicotyledons usually possess the following characters: the plants begin with two seedling leaves, the cotyledons (whence the name di-cotyledons); the leaves are usually netted-veined. The stem is usually thicker below than above, with the vascular bundles arranged to form a cylinder inclosing a

pith center; as growth proceeds new cylinders are formed, and since the vascular bundles formed in spring have thinner walls than those formed in late summer and fall the annual growth becomes visible as a concentric ring. A taproot is usually present; the parts of flowers are in fours or fives.

The dicotyledons are now generally regarded as more primitive than the monocotyledons and as their probable ancestor.



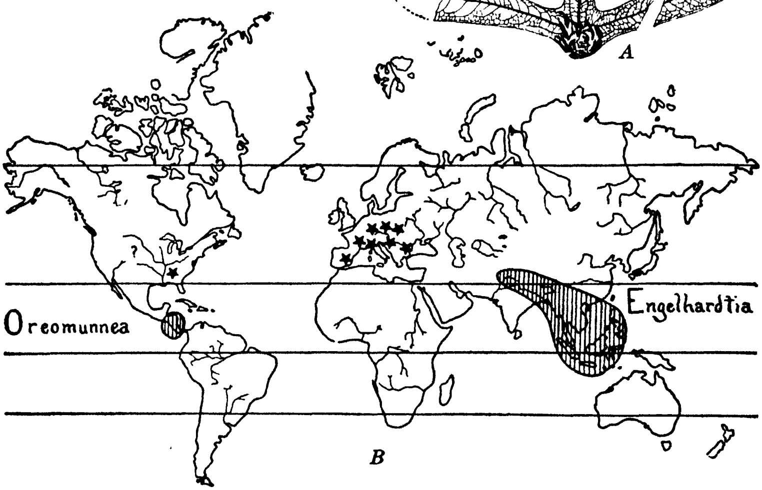


FIG. 44. — *A*, a fossil relative of the walnut family, *Engelhardtia* (*Oreomunnea*) *mississippiensis* Berry, from the Eocene of Mississippi (× ½). *B*, sketch map showing the existing distribution of Engelhardtia (vertical lining) and fossil occurrences (stars). There is here an indication of movement southward as the northern regions became colder, and of the obliteration of this tropical genus from Europe, where southward migration during the glacial period was prevented by the transverse shores of the Mediterranean Sea. (From Berry.)

1. One of the most primitive of the dicotyledons is the American tulip tree, *Liriodendron tulipifera*, a beautiful forest type, of eastern North America, reaching a diameter of four to twelve feet, and a height of sixty to one hundred and ninety

feet. The closely related species, *L. chinensis*, occurs in eastern Asia. These are the sole survivors of the genus Liriodendron which had formerly a far wider distribution. Appearing first in the Upper Cretaceous in great variety and number of species, it flourished during this period in North America from Wyoming to New Jersey and in Greenland. In Tertiary time it still extended its range over Iceland and Eurasia; but the cold climates of the Pleistocene forced the last remnants of Liriodendron southward in Europe and finally cut them off on the shores of the Mediterranean Sea, which, with the Alps, acted as a transverse barrier to the farther retreat of this and many other types. Thus is explained the paucity of dicotyledons in Europe as compared with North America and eastern Asia, where retreat southward during the ice age was not thus cut off by high mountains or transverse shores. This late restriction of distribution is also seen in Engelhardtia (Fig. 44).

2. Sassafras, like Liriodendron, is also a ditypic genus now restricted to *S. officinalis*, confined to eastern North America, and a closely related Chinese form. Like Liriodendron, it is the last representative of a large group which flourished at least throughout North America and Europe since the Lower Cretaceous, but could survive the cold Pleistocene climate only in North America and eastern Asia. It is known first from the Lower Cretaceous of Virginia, Greenland, and Portugal, later from the Upper Cretaceous of North America (occurring from the Rockies to New Jersey), Greenland, and Europe, and it continued to have a cosmopolitan range throughout the Tertiary; a late Pleistocene species from France and Italy is almost identical with the living form.

3. The poplar (Populus) is known to have lived during Lower Cretaceous time in Virginia and Greenland, throughout North America and Greenland during the Upper Cretaceous, and in Europe, North America, and Arctic lands in the Tertiary.

1. What is the especial feature that characterizes the angiosperms? What is the difference, indicated by the derivation of the words, between angiosperms and gymnosperms?

2. Describe a typical flower. Show that each part is a modified leaf.

3. Outline the method of fertilization.

4. What is the sporophyte stage of an angiosperm? What the gametophyte? How does their relative importance among angiosperms compare with it among the mosses? Among the ferns?

5. In what geologic age did angiosperms appear?

6. How are angiosperms divided?

7. Name three features which distinguish a monocotyledon from a dicotyledon.

8. Discuss one example of the former class, giving its geographic and geologic range.

9. Discuss one example of the dicotyledons, giving geographic and geologic range.

10. Why are ditypic genera, like Liriodendron and Sassafras, considered primitive?

Evolution of Plants

A plant in its simplest form is essentially a minute mass of protoplasm encased in a firm rounded cell wall. A comparable stage in the animal line is to be observed among the flagellates. Such an organism is a minute laboratory for the carrying on of the fundamental activity of all life — the storage and expenditure of energy. Some of the energy is used in division of the cells, and the many-celled plant came into existence when some of the cells remained in contact after division. The resulting larger organisms possessed more surface exposed to the sun's rays and in contact with food in solution in ocean or soil, and thus could avail themselves of larger stores of energy.

Subdivision of labor developed among the cells of these larger plants. Among the larger thallophytes certain cells have a protecting function, others are reproductive, others manufacture starch. Size, however, is limited by the relation of the mass and weight to the strength of the supporting structure. The cellular wall of the simpler water-dwelling thallophytes, such as Spirogyra, is very tender. In larger algæ, like the Devil's Apron, it is much stronger but the water supports its weight; it cannot support its own weight in air. Accordingly when plants branched out upon the land, the cellular structure grad-

ually evolved into a stronger type, the vascular, with the cells arranged end to end in a series of minute pipes bound together in bundles. It is thus seen that one of the changes necessary in the development of a land flora was the change from a cellular structure to a vascular — a change that opened up possibilities of increase in size, that laid the foundations for the mighty trees of the Carboniferous forests and the giant redwoods of our western states.

There was another difficulty that plants had to meet in adapting themselves to land. They must develop a resistance to the drying-out quality of the air. The earliest plants were tied to the water; water gave them food, held them up against the pull of gravity, kept them from drying up and enabled them to reproduce. This is the stage of the thallophytes. The first step in the development of a land flora was probably taken by some early group of fresh-water algæ. In ponds subject to annual drought, the more plastic forms of life would feel an impetus to extend their cells in contact with the damp soil down into root hairs, while the cells that came into contact with the air would tend to develop a thickened surface. An early stage in such adaptation to air may be seen in the liverworts. These are but slightly resistant to dry air and must consequently live in moist areas, such as the edge of waterfalls.

The change from a cellular to a vascular structure, and the larger plant thus rendered possible, led to the development of roots that could secure a foothold deep in the soil. This step was taken by the Pteridophytes. Mammoth tree ferns reared lofty stems and developed deep-branching roots in the late Paleozoic.

Only slowly did life win even a measure of freedom from its dependence on water. Long after the purely vegetative phases of a plant adapted themselves to life on land, water remained necessary for the dispersal and union of the reproductive elements, the male and female gametes. The mosses and ferns, with a resistant cuticle and in harmony with dry-land conditions, still depend on rain or dew for the union of the gametes. It is

only the Spermatophyta which have evolved a device which has finally freed them of the necessity of external water for the process of fertilization. Equipped with this independence, they may radiate into all kinds of terrestrial habitats that the earth affords.

Bryophyta, Pteridophyta, and Spermatophyta as Rock-Builders

Since in these terrestrial phyla the cellulose cell walls are denser and more resistant to decay than those of the thallophytes, they may under proper conditions be preserved. Such deposits — peat, lignite, coal — are known from the late Devonian to the present. Even in coal, one may occasionally see with the unaided eye fragments of wood along the bedding plane, while across the stratification plane cross-sections of twigs appear as glistening black lenses. Coal deposits are especially abundant in the Mississippian, Pennsylvanian, Permian, Triassic, Cretaceous, and Tertiary.

1. Divide plants into phyla, classes and all minor subdivisions, giving an example of each.
2. What is the basis of this classification? How does the increase in complexity of organization correspond to the order of appearance in geologic time?
3. Outline the changes in the relation of sporophyte to gametophyte stages from the thallophytes to the spermatophytes.
4. In what mineralogical state do the majority of fossil plants occur? Outline the process which changes the living tissue of the plant to this condition.
5. Give some necessary steps in the evolution of a land flora.
6. Discuss the Bryophyta, Pteridophyta, and Spermatophyta as rock builders.

ANIMALS

INTRODUCTORY

THE acquirement of a supply of energy is an essential of all life. Plants as a rule derive this from the sun, and animals in turn from plants or, more indirectly, from plant-eating animals. That "all flesh is grass" is indeed true. Plants transform the kinetic energy of sunlight into the potential energy of carbohydrates; this can again be made kinetic when oxidized as in the digestion of food. The food glucose ($C_6H_{12}O_6$) + O_{12} (taken in by respiration) = the waste gases ($6\,CO_2 + 6\,H_2O$) + the energy-giving calories derived by plants from the sun.

The lines along which life has branched during its existence on earth have varied much in capacity to evolve higher forms. Plants developed hard protective parts which to a great extent cut them off from external stimuli and made freedom of movement impossible. Animals, on the other hand, never quite abandoned the ability to move freely. Moreover, while many groups developed hard external parts which in some measure protected them from impacts from without, there remained in each phylum other branches which escaped these limitations. Anticipating the developments in historic warfare, they eliminated the protecting but cumbersome armor, and met their defensive and offensive needs by means of more responsive muscles through a higher type of nervous system.

The three main branches along the animal pathway are those of the mollusks, the arthropods, and the vertebrates. Of these the more progressive branches terminate at present in the squids and devilfish (Dibranchiata) of the mollusks, the insects of the arthropods, and the mammals of the vertebrates.

All the way from the protozoöns to the vertebrates, the advance of life may be measured, as in human social institutions,

by subdivision of labor. Among the Protozoa, the single cell which constitutes the entire animal performs all the functions which in the vertebrate are accomplished by millions of cells working through hundreds of organs. Upon this division of labor, as well as upon the variations in the organs through which the work is performed, is based the classification of the animal kingdom into great groups or phyla.

CHAPTER VI

PHYLUM I. PROTOZOA

The Protozoa are simple, one-celled, aquatic animals consisting of protoplasm. They are usually microscopic, but there are great extremes in size. Some have a diameter of only $\frac{1}{10,000}$ of an inch, while *Porospora gigantea*, a parasite on the intestine of lobsters, is two-thirds of an inch in length and Nummulites may be a giant of over two inches' diameter. The same species may vary much in size according to the supply of food. A living species of Dileptus varied from a length of 80 mm. when normal to 10 mm. when starved. When hard parts are present, they may be secreted within the cell or upon the surface of the protoplasm. They consist of chitin in some of the Sarcodina, of cellulose in the Dinoflagellata, of calcium carbonate in the Foraminifera, and of silica in the Radiolaria. Protozoa are the most abundant aquatic animals.

Derivation of name. — Protozoa > Greek *protos*, first + *zoon*, animal; in this phylum occur the first or lowest animals.

The Protozoa are divided into the following four classes, of which only the Sarcodina and possibly the Mastigophora have fossil representatives:

Type of phylum, ***Amœba proteus*** **(living) (Fig. 45).**

Amœba is a microscopic mass of jelly-like protoplasm, about 0.2 mm. in diameter, with a clear, usually thin, outer layer and a granular inner portion, the granules being mostly proteid and

fat particles. Within this granular portion is a darker, rounded body, the nucleus, and a rounded, pulsating, clear space, the contractile vacuole.

It secretes no skeleton, and is free-moving and abundant at the bottom of fresh-water pools and ponds among decaying vegetation. It is irregular and variable in outline, continually altering its shape by slowly pushing out and withdrawing various parts of its body; these temporary finger-like processes are called pseudopodia. *Movement* takes place by the gradual streaming of the entire substance of the amœba into the projections from one side, and is thus practically a flowing process, "the upper surface" (in *Amœba verrucosa*) "continually passing forward and rolling under at the anterior end so as to form the lower surface."

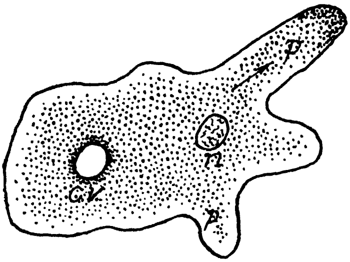


FIG. 45. — The fresh-water protozoön, *Amœba proteus*. It is shown moving in the direction of the arrow. *n*, nucleus; *c.v.*, contractile vacuole; *p*, pseudopodia. Very much enlarged.

Its **food** consists of those entire minute animals (other protozoöns), or plants (bacteria and diatoms), or any organic particles with which the pseudopods, or main body portion have come into contact. The amœba pursues such prey as long as it is in contact with it, rolling it ahead in its attempts to catch it, then sending out pseudopodia on each side to surround it. Finally, if the prey has not escaped, the amœba succeeds in surrounding it with its side pseudopodia and sends out from its upper surface a thin film of protoplasm over it, thus completely engulfing it. This food is pressed into the soft substance and passes gradually into the interior.

Digestion. — With the food-victim a certain amount of water is taken in by the amœba; this water with the victim forms a "gastric vacuole" or an improvised stomach, surrounded on all sides by a wall of living protoplasm. From this protoplasm there soon begins to form an acid secretion, probably hydro-

chloric acid, which thus gradually changes the chemical nature of the water of the gastric vacuole and kills the prey which it incloses. It is probable that the product of the digestive action of this acid is the formation of soluble peptones similar to the products of proteid digestion in the higher animals. This is followed by a digestive ferment like trypsin, acting in an alkaline medium.

The manufacture of the acid secretion is intimately connected with the chromatin material of the nucleus, for digestion does not take place when the nucleus is absent. "Protozoa evidently have the power of secreting different kinds of ferments in response to the stimulus of different kinds of living food particles." Some types of Protozoa can create starch-dissolving ferments or fat-emulsifying ferments, though other species throw the starch grains out of the body with other indigestible parts of the food.

Assimilation. — "The granules that are formed by the breaking down of the food particles through the digestive process are ultimately distributed by means of the protoplasm which streams to all parts of the protozoön" through the animal's rolling method of progression and by osmosis. "Some are probably converted directly into protoplasm by an assimilative process that is as little understood in these forms as in the Metazoa."

Excretion. — The undigested food particles pass outwards into the surrounding water, and are left behind as the amœba rolls forward. Thus, whatever part of the amœba's body touches food becomes mouth, whatever portion the food particle enters becomes digestive cavity, and the undigested material may leave from any part of the surface.

It is probable that the contractile vacuole is the chief organ of excretion, that by its means the animal rids itself of the waste products of assimilation and metabolism, such as urea and carbon dioxide.

Respiration, or the exchange of gaseous waste products for oxygen, takes place through the entire surface of the body,

most of the oxygen being obtained in this way, though probably most of the carbon dioxide is thrown off by the contractile vacuole.

There is no trace of a **nervous system,** though the animal displays many of the reactions to stimuli which higher forms possess. It is sensitive to chemical changes in the water surrounding it and to heat, moving away from the chemically changed area and from the source of heat. It moves away likewise from the source of strong light and toward the negative pole when the water containing it is charged with electricity. It avoids mechanical obstacles in the water by reversing the flow of its protoplasm into the opposite direction. Thus mechanical, chemical, and electrical stimuli and variations in heat and light control the direction of movement.

Reproduction is mainly by simple division. When more food is taken in than is required for maintaining the size unaltered, a constriction appears dividing the entire amœba, including the nucleus, into two parts, thus producing two cells or two individuals. Each individual amœba is a single cell, that is, it consists of a mass of protoplasm with an included nucleus. All animals higher than Protozoa, as well as all higher plants, consist of many such cells, usually with some more or less firm protective or strengthening substance.

Basic life processes. — It is not as a single cell with varied characteristics and functions that a protozoön should be regarded, but as an animal unified, possessed of a " will to live," illustrating in their simplest form the fundamental activities of all animals. Amœba selects food, eats, and assimilates it. Though the food vacuoles are only temporary stomachs, yet digestion is fundamentally similar to that of other animals, being performed with the aid of a solution of HCl, and, in some forms, of fat-dissolving ferments. From this assimilated food the animal derives energy and the material for further growth. Like all more highly organized animals, Amœba excretes solid, liquid, and gaseous waste products. It breathes, *i.e.*, it throws off carbon dioxide and takes in oxygen from the air in the sur-

rounding water. Though lacking a nervous system, the protozoön displays that fundamental characteristic of all living matter called irritability. This means that it responds in some way, such as alteration in form or reversal of direction of movement, to those more or less sudden changes in the environment which may be called stimuli. Reproduction is by the basic process of cell division. Thus Amœba exhibits in their simplest expression those characteristics of all animal life which tend to preserve both the individual and the race.

1. How do animals acquire the energy necessary for existence?
2. Upon what fundamental basis are animals subdivided?
3. If Amœba is available, it should be examined under a compound microscope, its shape and movements noted.
4. Give the size and structure of the animal. Illustrate with a sketch.
5. Where does it live? What does it feed upon?
6. How is food procured? How is it digested, and how is the waste thrown off?
7. How is the food assimilated?
8. How does the animal breathe?
9. Does Amœba possess nerves? How does it respond to stimuli?
10. Describe its reproduction.
11. Where do Protozoa occur?
12. What is meant by calling protozoöns one-celled animals?
13. What fundamental life processes of all animals find their simplest expression in Protozoa? Are any lacking here that are present in higher animals?

CLASS A. SARCODINA

These are marine or fresh-water Protozoa with a body which alternately protrudes and retracts first one and then another part into finger-like processes — the pseudopodia. A contractile vacuole is present in some fresh-water but not in marine forms. Reproduction is by binary or by multiple (spore-formation) fission. The members of this class are relatively large, many being visible to the naked eye. Some of the fossil forms especially, as Nummulites and Orbitoides, attain proportions which are gigantic for Protozoa.

Derivation of name. — Sarcodina > sarcode > Greek *sarx* (*sark-*) flesh. Sarcode was the name applied by Dujardin to what is now called protoplasm.

The Sarcodina are divided into the two subclasses:

1. Rhizopoda.
2. Actinopoda.

SUBCLASS 1. RHIZOPODA

Usually creeping forms with branched pseudopodia (whence the name from Greek *rhiza*, a root, + *pous* (*pod-*) foot). This is subdivided into the orders —

1. Lobosa. — Amœboid (changeable) forms, usually without shells. Unknown in the fossil state. The genus Amœba is the most common representative.

2. Xenophyophora. — This includes some deep-sea forms with a peculiar internal structure and a skeleton composed of foreign bodies, such as sand grains, sponge spicules, etc. (whence the name from Greek *xenophyra*, foreign bodies, + *pherein*, to bear). Unknown in the fossil state.

3. Foraminifera. — Skeleton (usually referred to as a test in all protozoöns) present, composed of calcium carbonate, more rarely of sand or of chitin, forming one or more chambers; this is perforated by one or more openings (whence the name from Latin *foramen*, a hole, + *ferre*, to bear). Pseudopodia are long and slender, uniting at intervals. Most Foraminifera are bottom-living forms, using their net-like pseudopodia to capture food. They crawl slowly about or are attached to various objects at the sea bottom. A few (26) species have become adapted to a pelagic existence. All but one of these belong to the two families Globigerinidæ and Globorotaliidæ.

Reproduction in the Foraminifera is both sexual and asexual. The sexually produced test results from the conjugation of zoöspores. It has a microspheric first chamber (proloculum). With increase in size and in number of chambers the nucleus also divides, often resulting in a greater number of nuclei than

chambers. In the adult, each nucleus takes some of the protoplasm and forms a megalospheric first chamber (proloculum) larger than the microspheric; this develops into an adult test similar to the microspheric test, but smaller. In this adult form there is a single nucleus which moves forward so as to occupy the middle chamber; this finally divides, each portion taking some of the protoplasm; a further division results in zoöspores, or the animal may first continue for some generations reproducing asexually. The life cycle, consisting of an alternation of generations, is thus completed.

The majority of Foraminifera are marine; a very few of the simpler forms live in brackish, or even fresh water. They are now found in all seas (seldom below 2500 fathoms, since by the time such depths are reached the tests are dissolved).

Foraminifera occur from the Cambrian to the present. Owing to their importance as indices of the age of oil-bearing strata, Foraminifera, or "forams" as they are usually called by workers in this field, have received much detailed study.

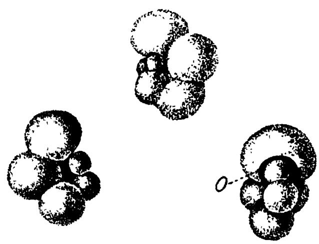


FIG. 46. — The lime-secreting protozoön, *Globigerina æquilateralis* Brady, from the Gulf of Mexico. This species is world-wide in its distribution, in both tropical and subtropical waters. Three views of the same specimen (much enlarged). The greatest mass of protoplasm was extended through the large opening (*O*).

Globigerina (Fig. 46).

Cretaceous to present.

This differs from Amœba in the possession of a calcareous support, the test. This test is composed of several globular chambers arranged in an irregular spiral (whence the name from Latin *globus*, a ball, + *gerere*, to carry). It also differs from Amœba in the length and delicacy of pseudopodia, which unite with each other at intervals. The chambers are somewhat glassy in appearance, and are pierced by numerous pores through which, as well as through the large opening from the largest chamber, the pseudopodia are extended. The protoplasm is

perfectly continuous throughout all the chambers. The food consists mostly of microscopic plants, such as diatoms and algæ, more seldom of the minute copepod crustaceans; these are enveloped and digested by the net-like pseudopodia.

Globigerina typically lives floating at the surface of the ocean, spreading out its pseudopodia in all directions around it. At the death of the individuals, the tests fall to the sea bottom, and accumulate in vast layers, forming the globigerina oozes.

Although known from the Triassic to the present, it occurs but sparingly in the Mesozoic.

1. Examine the specimens under the compound microscope (these should include thin sections of chalk, and some globigerina ooze or sand scraped from such shells as those from the Paris Basin, from sponges or from corals).

2. Sketch (*a*) Globigerina, (*b*) Textularia (Cambrian to present), usually cone-shaped with two rows of alternating, communicating chambers, (*c*) Rotalia (Cretaceous to present), chambers of test forming a flat spire. For examining the chambers use transmitted light. Label chambers, large and small openings.

3. Did the protoplasm occupy one or more chambers?

4. What is the food of Globigerina? How does its manner of capture differ from that in Amœba?

5. Describe the reproduction.

6. What is meant by "alternation of generations"?

7. What is the significance of the name Foraminifera?

8. Is chalk of shallow or deep water origin? Reasons.

9. Where do most Foraminifera live?

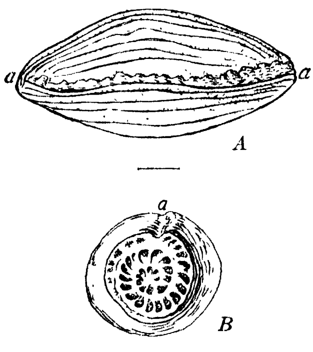


FIG. 47. — The protozoan skeleton, the Fusulinid *Triticites secalica* (Say), abundant in the shallow seas covering Kansas during a part of the Pennsylvanian period. *A*, surface view showing the fissure-like aperture (*a–a*). *B*, cross section showing the internal chambers and the aperture (*a*). Both enlarged; note scale of *A*.

Fusulinidæ (Fig. 47). *Pennsylvanian and Permian.*

The test is gigantic, like a grain of wheat in shape and size. This spindle-shaped form suggests the name (Latin *fusus*, a

spindle). Symmetry is bilateral; each chamber extends from end to end so that each whorl completely covers the preceding one. The aperture is in the form of a fissure.

These are exceedingly abundant in the Pennsylvanian and Permian of North America, Europe, and Asia.

1. Sketch (*a*) entire fossil with opening upwards, (*b*) cross-section, showing method of coiling.

2. Comparing with Globigerina, how did the living animal probably procure its food?

Nummulites (Fig. 48).

Pennsylvanian to present.

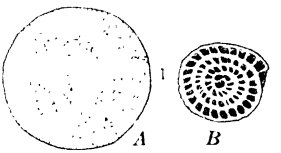


Fig. 48. — The skeleton of a marine protozoön, *Nummulites*, from the Eocene of Egypt. A very small specimen enlarged. *A*, surface view of the coin-like shell. *B*, section parallel to the flat surface.

Test flattened, lens- or coin-shaped (whence the name from Latin *nummulus*, diminutive of *nummus*, a coin). Internally there is a spiral series of chambers. Each whorl completely incloses the preceding by means of a lateral prolongation of the chambers. The aperture is an inconspicuous slit at the inner margin of the last chamber. In Nummulites the increase in size is mainly on the periphery, in the Fusulinids, it is mainly axial. A large and a small form are usually found associated in the same rock; these most probably are the large sexually produced test, and the small asexually produced test of the same species.

Nummulites occur from the Pennsylvanian to the present, but sparsely outside the Tertiary. The one or two forms now living, as off the southeast coast of Asia, are tropical and subtropical. Nummulites attained their maximum abundance during the Eocene, making limestone masses, — nummulitic limestone, up to several thousand feet in thickness, in the East Indies, Japan, South Asia, South Europe, and North Africa. The largest species in these rocks attains a diameter of 60 mm.; the smallest, 2 mm. Associated with these Nummulites are other marine forms, such as mollusks and corals. The great pyramid of Cheops is built of this limestone.

Many authors are using the older name Camerina in place of Nummulites.

1. Sketch (*a*) surface view, (*b*) longitudinal section, (*c*) transverse section. A thin section made from nummulitic limestone will usually give the above sections.
2. How does this differ in its manner of coiling from the Fusulinids?
3. What is the significance of the name?
4. When and where did it occur most abundantly?
5. Account for the large and small forms usually found associated in the same rock.

Lepidocyclina (Fig. 49).

Eocene to Miocene.

The general shape of test is very similar to that of Nummulites, but the chambers are smaller, much more numerous and complicated. This, like the two preceding genera, is one of the gigantic forams.

Lepidocyclina is very abundant in the lower Tertiary. In the Gulf States of North America it makes up in places the entire rock, as does Nummulites in the Mediterranean region of Eurasia and Africa. The Vicksburg or "Orbitoides" limestone of Oligocene age attains a considerable thickness in Alabama.

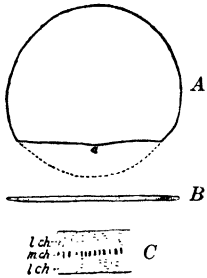


FIG. 49. — A protozoan calcareous skeleton, *Lepidocyclina* (formerly called *Orbitoides*), abounding in the Oligocene Sea at St. Stephens, Alabama. *A*, surface view (× ½). *B*, vertical section along line *a*. *C*, section of another specimen much enlarged; *m.ch.*, median chambers; this row is much larger than the ones (*l.ch.*) upon either side; *l.ch.*, lateral chambers.

1. Sketch (*a*) surface view, (*b*) longitudinal section, (*c*) transverse section.
2. How does this differ from Nummulites?

SUBCLASS 2. ACTINOPODA

Usually floating forms with ray-like, unbranched, rarely changeable pseudopodia provided with an axial thread (whence the name from Greek *aktis* (*aktin-*) a ray, + *pous* (*pod*) foot). This is subdivided into the orders:

1. Heliozoa, commonly called the "sun-animalcules" because of the fine ray-like pseudopodia (whence the name from Greek *helios*, sun, + *zoon*, animal). — These do not possess the chitinous central capsule characteristic of the Radiolaria. They are almost confined to fresh water. Unknown in the fossil state. Example, Actinophrys.

2. Radiolaria (Fig. 50). — The body is composed of a central mass of protoplasm inclosed in a perforated, chitinous membrane, the central capsule, and is continuous through this with a layer of protoplasm outside the membrane; this layer gives off ray-like pseudopodia (whence the name from Latin *radiolus*, a little ray). There is usually present, in addition to the central capsule, another skeleton, beautiful and delicate; this is secreted by the protoplasm, usually without, sometimes extending or originating within the central capsule; it consists of isolated spicules, bars or latticework made of silica (opal) (Fig. 50), or rarely of acanthin, a substance allied to chitin. When the silica is secreted it is thrown down in the protoplasm all at once, apparently at the supersaturation point.

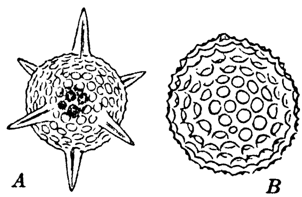


FIG. 50. — Siliceous skeletons of Radiolaria, from the Miocene of Maryland. *A*, *Hexalonche microsphæra* Vinassa (× 130). *B*, *Cenosphæra porosissima* Vinassa (× 160). (From Martin.)

The Radiolaria are marine organisms, floating at the surface of the ocean, or even at abyssal depths, and present in all climates. In some deep parts of the Pacific and Indian oceans these tests, falling after the death of the animal, accumulate on the sea-bottom, forming a siliceous deposit, known as "radiolarian ooze."

Radiolaria occur from the pre-Cambrian to the present.

CLASS B. MASTIGOPHORA (FLAGELLATA)

Protozoa with a definite body outline, the body protected in some species by a skeleton of cellulose or chitin, but usually

naked. Organs of locomotion and of food-capture in adults are the flagella — slender threads capable of whip-like lashing movements (whence the name from Greek *mastix*, a whip, + *pherein*, to bear). Euglena is an example.

Fossil representatives of the order Dinoflagellata with a cellulose skeleton are reported from the flint in the European Cretaceous (Bütschli).

CLASS C. SPOROZOA

Parasitic Protozoa. There are no definite organs of locomotion or of food-getting in the adult. Reproduction is typically by the formation of seed-like bodies, — spores (whence the name from Greek *spora*, seed, + *zoon*, animal). Each spore contains one or more minute germs, — sporozoites. Unknown in the fossil state. Gregarina and Plasmodium are two of the common genera. Three different species of the latter may cause human malaria.

CLASS D. INFUSORIA

Protozoa with a definite body outline. The organs of locomotion and food-capture during all or a part of their active life are cilia — small vibratile threads, smaller and more numerous than flagella. There is a vegetative large macronucleus and a smaller generative micronucleus. (The name was originally applied to all those minute plants and animals that make their appearance in infusions of decaying organic substance, but is now restricted to Protozoa as defined above.) Unknown in the fossil state. Examples are Vorticella, Paramœcium, and Stentor.

Evolution of the Protozoa

Since energy is essential in the continuance of life, and organic food is the primary source of all energy in animals, it is to be expected that an animal group will in time develop various modi-

fications of form in response to the exigencies of food-getting. These one-celled animals have met this need by radiations into four main directions:

1. The protoplasm sends out more or less temporary food-procuring projections, the pseudopodia. This group is called the Sarcodina.
2. The protoplasmic projection is confined to one or more permanent extensions, the flagella, in the Mastigophora.
3. The protoplasm is extended outward into numerous permanent cilia in the Infusoria. Some degenerate sessile forms have no cilia in the adult.
4. A large group of protozoöns became parasites within many-celled animals. This group is the Sporozoa.

Protozoa as Rock-Builders

Rock building is naturally confined to the lime- and silica-secreting orders of Foraminifera and Radiolaria.

The modern Globigerina oozes are composed very largely of representatives of the pelagic families Globigerinidæ and Globorotaliidæ. They occur from the edge of the continental shelf to a depth of 25,000 fathoms. Many other families are represented in the oozes especially at depths from 1000 fathoms up, but the pelagic species greatly predominate.

Although Foraminifera were present from Cambrian times, reproduction apparently was too slow to enable the tests to enter largely into the composition of rocks before the Pennsylvanian. During this period and the Permian, many species of the family Fusulinidæ formed solid masses of "Fusulina" limestone at numerous horizons throughout the Northern Hemisphere. Such limestone abounds from California and British Columbia to Illinois, in Europe north into Spitzbergen, and east through the Himalayas into China and Japan.

The Cretaceous is the next period during which the forams become important as rock-builders. At this time it is the microscopic forms which compose the limestones. The rock is composed of tests too minute to be seen by the unaided eye and of their broken fragments; this friable limestone is called chalk.

These Cretaceous chalk beds were formed in shallow marine waters, at a depth which probably did not exceed 50 fathoms; this is indicated by the presence in the chalk of such pelecypods as Inoceramus and Pecten and by the intercalated sandstones. The Comanche (Lower Cretaceous) limestones of Texas are in places largely chalk. But it is the Upper Cretaceous which is especially characterized by the presence of chalk. In the United States it increases westward from the Atlantic region where it is practically lacking, through the Eastern Gulf region (Selma chalk, for example, 1000 feet thick in Alabama, Mississippi, etc.), reaching its most widespread development in Texas (Austin chalk, 600 feet) and northward as the Niobrara chalk, 200 feet, through Kansas, Wyoming, etc. These formations are not composed of chalk throughout. In northwestern Europe, especially England and France, the Upper Cretaceous chalk is several hundred feet thick. As with the American chalk, this grades into chalk marl in places, with the admixture of clay, and in other localities grades into a sandstone.

During the Eocene many species of " nummulites " abounded in the greatly enlarged Mediterranean known as the Tethys Sea. This sea covered northern Africa, southern Europe, and extended east through southern Asia over the present Himalayas to Japan and the East Indies. Throughout this Mediterranean " nummulites " tests are the principal constituents of limestone strata, often several hundred feet thick, at times to the exclusion of all other shells. The great pyramids at Gizeh, five miles southwest of Cairo, were built of such beds, while the Sphinx was carved out of such strata in place.

The Upper Eocene limestone of Florida is composed of large forams, especially various species of Lepidocyclina. This Ocala limestone varies in thickness from 150 to 400 feet.

The Lower Oligocene, especially the Vicksburg limestone, is in places composed almost entirely of *Lepidocyclina* (formerly *Orbitoides*) *mantelli*. This extends from Louisiana to Florida. In the latter state it is 30 feet thick and is known as the Marianna limestone.

Representatives of the silica-secreting order Radiolaria are to-day forming " radiolarian ooze " in some deep parts of the Pacific and the Indian oceans. Though known from the pre-Cambrian to the present, radiolarians are rarely found to enter largely into the formation of strata. Rocks of such composition are known as radiolarites. They have been reported from the Mississippian of the Rhine district and of Great Britain. In the Jurassic of the Alps occur beds of red flints and jaspery slates which consist almost entirely of tests of radiolarians. In the city of San Francisco in California are such radiolarites of Miocene age. The Barbados earth, Miocene in age and covering large areas in the Barbados Islands, resembles very closely the modern radiolarian ooze and is probably a deep-sea deposit. Heliodiscus and Astromma are two genera found here.

In the " Barbados earth " the siliceous skeletons of radiolarians still retain their originally amorphous condition. Usually these skeletons are dissolved soon after burial in the rocks by percolating waters containing alkali and may be redeposited as chert. The chert nodules of the upper Cretaceous chalk are, at least in part, due to these skeletons.

1. Give a detailed classification of the Protozoa (in classes, subclasses and orders), with an example of each.
2. What is the principal external factor in the radiation of the Protozoa? Into what four directions have they radiated?
3. When did Foraminifera first become important as rock-builders?
4. Are the majority of forams bottom-dwellers or pelagic? By which group are the Globigerina oozes of to-day formed?
5. Give the distribution of the "Fusulina" limestone, the Cretaceous chalk, the nummulitic limestone.
6. Are Radiolaria important as rock-builders? List some recent and fossil examples.
7. How do radiolarian and Globigerina ooze differ in chemical composition?
8. What classes of Protozoa have been found fossil?
9. What orders of Protozoa are most important as Index Fossils? Explain their use in oil geology.
10. Describe the formation of chalk.

CHAPTER VII

PHYLUM II. PORIFERA (SPONGES)

Sponges are organisms consisting of many cells, plant-like in appearance and extremely variable in shape. Sponges growing side by side will frequently fuse into one mass, and almost any fragment of a sponge will grow into a perfect individual. They are fixed, aquatic, and usually colonial animals. Nearly all sponges are marine and are most abundant in the shallow parts of the ocean (Euspongia, Cliona); but some with a siliceous skeleton (Euplectella) occur in the abyssal portions. The green sponge, Spongilla, is the most common genus inhabiting fresh water; its natural color is a light gray, but it is usually colored green through the presence of algæ.

Typically a simple sponge looks like a hollow, attached vase; it consists of a cylindric body pierced by many canals which conduct water through the wall into a large central or paragastric cavity; this opens to the exterior by a large opening, the *osculum*. Water is drawn in through these many small canals and forced out through the large osculum. The canals are of three kinds, (*a*) the incurrent, leading from the outside into the wall of the sponge, (*b*) the flagellate or gastral, and (*c*) the excurrent, leading into the central cavity. The greater the depth of the water, the larger is the size of the incurrent canals.

The flagellate canals, the gastral layer, consist in all sponges of collar-cells; they are the principal organs for the *capture* and *digestion* of food.

The paragastric or central cavity may be very deep, often is very shallow, at times it may disappear so that the excurrent canals are upon the surface. Forms with one central cavity and one osculum are regarded as individuals, those with more

than one as colonies, but as it is difficult to distinguish between small oscula and large excurrent canals, the distinction of individuals from colonies is likewise difficult.

The sponge is not a colony of protozoöns, but an individual, for not until an osculum is formed can it feed and reproduce.

The **skeleton** consists of calcareous or siliceous spicules or of horny fibers, all developed at the base of the ectoderm, next to the mesoglœa (a non-cellular, gelatinous substance between the outer ectoderm and the inner endoderm). In the development of either calcareous or siliceous spicules there is first formed an organic thread at the center of the cell; around this axial thread the mineral matter is deposited as a colloid. The calcareous material, of almost pure calcium carbonate, becomes crystalline immediately upon deposition; each spicule behaves optically like a single crystal. In the siliceous spicules the colloidal silica is deposited in concentric lamellæ alternating with organic lamellæ; it does not become crystalline, but while the animal lives remains in the colloidal condition, a solidified colloid. It has been estimated that to form an ounce of siliceous spicules a sponge must pass a ton of sea water through its incurrent canals. The spicules of the Hexactinellida, when united, are joined by a secondary deposit of silica, but those of the Tetractinellida and Monactinellida are at times united by spongin, at others the spicules are enveloped in spongin, as in Chalina; finally in the Ceratospongida the spicules disappear and spongin alone remains, as is seen in the common bath sponge. Sponges are classified according to this skeleton.

The Myxospongida, with no skeletal elements, and the Ceratospongida, with skeleton of perishable fibers of spongin, can seldom be preserved as fossils. Practically all fossil sponges, therefore, belong to the orders secreting siliceous or calcareous spicules. In these orders fossils may be preserved in two states. If the skeletal framework is sufficiently firm to hold together after the death of the animal, and consequent disappearance of the soft parts, it may be preserved in its entirety, as for example in Prismodictya and Astylospongia. If, however, this

framework is composed of spicules so loosely bound together as to fall apart upon the disappearance of the soft parts, the scattered spicules alone will be preserved, as in Lyssacina, Cliona, and Renieria.

During fossilization the composition of a sponge skeleton may be greatly modified. In those forms with siliceous spicules the colloidal silica during fossilization may become cryptocrystalline, or be dissolved and carried off by percolating waters, or be replaced by calcium carbonate or some other substance. Likewise the calcareous spicules are often replaced by silica. Thus originally siliceous spicules may be converted into calcite and calcareous spicules may become silicified. Hence the distinction between siliceous and calcareous sponges in the fossil state depends upon form and not upon chemical composition.

When the siliceous spicules are so loosely bound together as to fall apart upon the decomposition of the soft parts of the animal, they will collect in the depositing sediment and where very abundant form porous siliceous beds. Usually the spicules have undergone partial solution in sea-water; this dissolved silica being redeposited as siliceous cement (chert) binds the remaining spicules together. Since the spicules are so very small, their presence is detected only by an examination of thin sections of the chert under a high-power microscope. The silica from such dissolved spicules and from other siliceous organisms is frequently redeposited as nodules of flint. The flint nodules in the Cretaceous chalk beds of England and France are notable examples.

Sponges are known from the pre-Cambrian to the present.

Derivation of name. — Porifera > Latin *porus*, a pore, + *ferre*, to bear; referring to the many minute incurrent canals penetrating the wall of the sponge.

The Porifera may be divided into the following classes:

Classes B and C are at times placed together into the Class Non-Calcarea. The old Class Silicispongiæ included the Hexactinellida, the Tetractinellida, and the Monactinellida.

Type of phylum, *Grantia ciliata* (living) (Fig. 51).

This "urn-sponge" is a hollow cylinder, somewhat spindle-shaped, about half an inch high by a quarter of an inch wide, attached

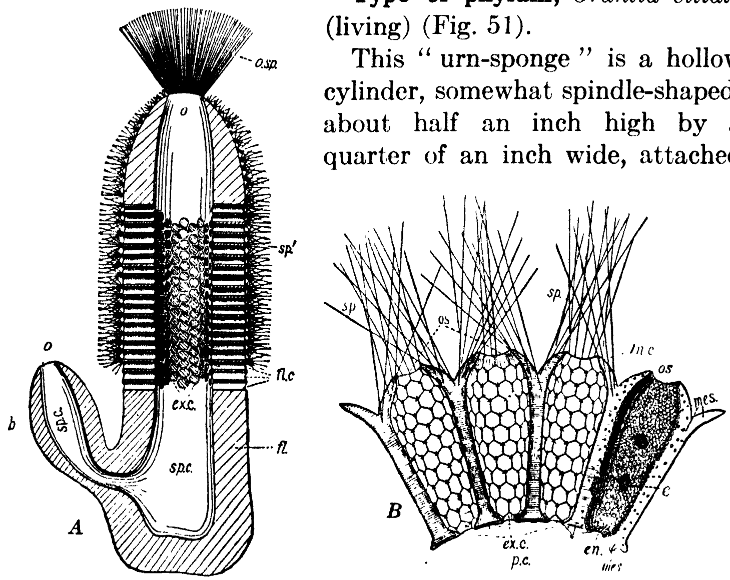


FIG. 51. — The common sponge, *Grantia ciliata*. The protecting and supporting spicules are calcareous. *A*, longitudinal section (× 10). *B*, transverse section (× 250). *b*, bud; *e*, eggs; *en.*, endoderm lining the flagellate canals, each armed with a single long cilium; *ex.c.*, excurrent canals; *fl.*, "flesh" of sponge; *fl.c.*, flagellate canals; *in.c.*, incurrent canals; *mes.*, mesoglœa, with scattered nuclei; *o*, osculum; *os.*, ostia, the outer openings of the incurrent canals; *o.sp.*, the very long spicules surrounding the osculum; *p.c.*, paragastric cavity; *sp.*, the long spicules surrounding the ostia; *sp'.*, the three-rayed spicules surrounding the flagellate canals; *sp.c.*, paragastric cavity shown in longitudinal section. (After Brooks, relettered.)

at base to some solid object. It is dull yellow to gray in color, with a large opening edged with spicules at its summit. It is found growing in tide pools from Rhode Island to Greenland and on the northern coasts of Europe.

The body wall consists primarily of three cell-layers, ectoderm,

endoderm, and mesoglœa. It is protected and a firmness given to the walls by a network of interlacing calcareous spicules. These are microscopic, spike-like calcareous bodies, with one to four rays. Each spicule is secreted by a single cell, or fused group of cells in the inner layer of the ectoderm, the remains of the cell being at times still distinguishable as a thin investment upon the surface of the full-grown spicule.

Food and Digestion. — The entire surface of the sponge is perforated by numerous, minute holes (ostia), through which a current of water enters the incurrent canals (lined with flattened ectodermal cells); from here it enters the elongate flagellate canals and passes out into the large central, or paragastric cavity by the short excurrent canals; these elongate flagellate or gastral canals are lined with endodermal cells, each of which is furnished with a protoplasmic collar from within which projects a thread-like lash, the flagellum; these cells are very similar to certain Protozoa — the Choanoflagellata, of the class Mastigophora. The flagella, having a stronger and swifter movement in one direction, moving in some forms ten times a second, cause the currents of water to pass from the outside through the incurrent, flagellate, and excurrent canals into the large central or paragastric cavity and thence out through the large opening, the osculum, at the summit of the sponge. The excurrent canal is in Grantia very short, a mere opening; in all the higher sponges, as in Spongilla, it is very long. The current of water carries with it many microscopic animals and plants, and food particles, which the collar-cells capture and ingest by means of the flagella and collars; each cell acts thus as a single protozoön. Wandering amœba-form cells take part in digestion; these can move from one part of the sponge to another. Thus digestion usually takes place within individual cells as in the Protozoa.

Circulation. — The transference of the digested particles of food from the digestive cells to the rest of the body is largely a process of simple osmosis, the cells having recently digested food being denser than the others; it is aided also by the very free

wandering of the amœba-form cells and to a less extent by the mesoglœa, into which some cells cast fluid or solid substances which are taken up by other cells.

All *waste*, such as undigested material, etc., is carried out through the osculum. Exchange of waste gases for oxygen is also effected by this current of water.

Around the outer edges of the incurrent and excurrent canals and the osculum are elongate cells (ectodermal and endodermal) which are contractile and thus represent **muscles.** These muscle cells effect the closing of these openings.

There is probably in all sponges a total absence of special **nerve** cells, and hence a great lack of coördination in cell movements, " thus the flagella of the collar-cells do not beat in unison like the cilia of the epithelia in higher animals, but each works independently of the others."

Reproduction takes place through the development of the sexual reproductive cells, spermatozoa and ova; these develop from the amœboid wandering cells of the mesoglœa, which take up their position directly below the flagellate cells. Both ova and spermatozoa are developed in the same sponge individual, though rarely at the same time. The amœboid cell, to form spermatozoa, divides into many small cells, each of which develops a long tapering tail. The amœboid cell, to become an ovum, simply becomes round and enlarges, and after a sperm has penetrated it, thus effecting impregnation, the ovum becomes inclosed in a brood-pouch made by the neighboring cells. In its development the ovum, after its impregnation, divides into two cells; these divide again and again, resulting in a hollow sphere, the *blastula.* In this shape, the embryo escapes to the exterior and moves about by means of flagella. Later the layer of cells from one side bends in against the layer of the opposite side, forming a double-walled cup, the *gastrula.* The opening of this gastrula cup, the blastopore, gradually closes, and at this stage of its development the young sponge becomes fixed by the side on which was situated the blastopore; an opening, the osculum, breaks through at the opposite end and the incurrent, flagellate,

and excurrent canals develop. The osculum thus does not correspond to the gastrula opening, as it does in the Cœlenterata, but is a later development opposite it.

Reproduction may be also asexual through the development of buds. A sponge may bud out a separate animal which may remain attached, forming a compound sponge, or may be detached from its parent and lead a separate existence.

1. Examine (*a*) an entire Grantia, (*b*) longitudinal and transverse sections under the compound microscope.
2. Show by diagram how the animal eats. What does it eat?
3. How is the food digested? assimilated?
4. How is respiration effected? excretion?
5. How are the soft parts of the body supported and the animal protected?
6. Are muscles present?
7. What is the nervous system like?
8. Describe the reproduction and the development of an animal from the egg to maturity.
9. If the genus Grantia were to become extinct, what record of its former existence and of its appearance would the rocks preserve?

CLASS A. CALCAREA

Skeleton of calcarous spicules (whence the name from Latin *calx*, lime). Spongin not present. At present these sponges occur in the shallower portions of the sea bordering the coasts; the fossil representatives (Middle Paleozoic to the present) lived under similar conditions, judging from the marly or sandy nature of the strata inclosing them.

Living examples are Grantia (described on page 135), and Sycon.

CLASS B. HEXACTINELLIDA

Skeleton of six-rayed siliceous spicules (whence the name from Greek *hex*, six, + *aktis*, a ray + Latin diminutive *ella*). When these spicules are united with each other, it is through the addition of secondary silica, never of spongin. To this class belong most of the fossil sponges. At present they are characteristic

of deep water, but the ancient forms, as the character of sediment and associated life forms indicate, lived mostly in comparatively shallow water. They are known as fossils, at least from the Cambrian to the present.

Euplectella aspergillum (Venus' flower basket) (Fig. 52, *B*). *Living.*

A tubular cornucopia-shaped sponge with a transverse, terminal sieve-like cap at its summit and an anchoring root-tuft at its base. The skeleton consists of siliceous threads, each of which is probably the greatly elongated ray of one axis of a three- to six-rayed spicule (the other rays being suppressed), cemented in adult life end to end to others by the addition of secondary silica. This process results in the formation of long, vertical, spiral, and circular threads which form a polygonal network around the central cavity. There is usually one ostium in each quadrangular interval. The vertical threads terminate in the conical root-tuft which forms the base. Upon the outside there are ornamental spiral ridges (whence probably the name from Greek *eu*, well, + *plektos*, twisted). It grows at considerable depths in the ocean fastened by the penetration of the stiff threads of the root-tuft into the mud or ooze. This species was dredged by the Challenger Expedition from a depth of 95 fathoms, and *E. crassistellata* from a depth of 2750 fathoms.

1. Sketch a side view of the entire specimen, labeling cap, root-tuft, ostia.
2. What is the composition of the skeleton? function of the root-tuft?
3. Give the probable origin of the long threads.
4. Describe the process by which Venus' flower basket could leave a record of itself in the inclosing sediments.

Prismodictya (Fig. 52, *A*). *Devonian and Mississippian*

An elongate, slender, gradually expanding, eight-sided prism; each prism-face reticulated by the spicular threads, which are arranged regularly in larger and smaller quadrate meshes situated one within another. Found as internal molds.

This sponge was very similar to Venus' flower basket, though

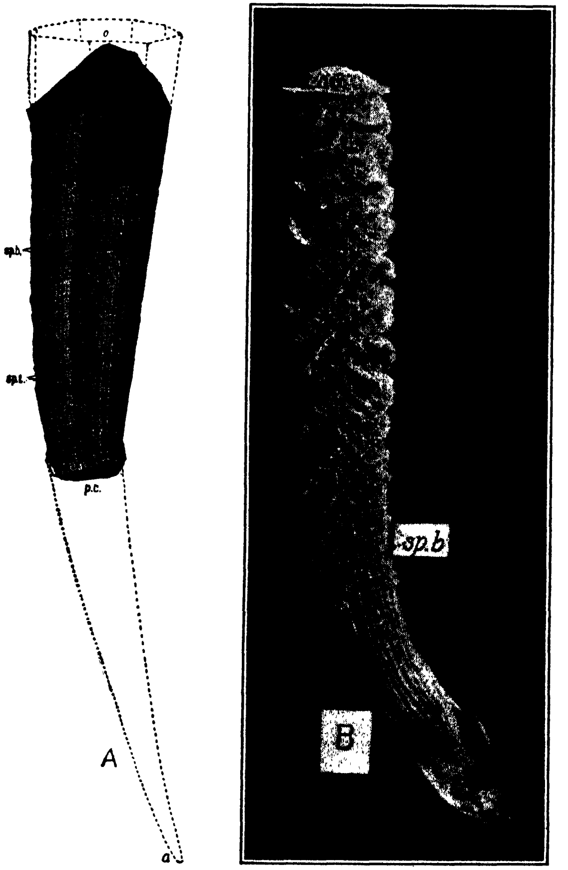


FIG. 52. — Comparison of a fossil and a modern glass sponge. *A*, internal mold of *Prismodictya prismatica* Hall; very abundant in the ocean covering New York state during the Upper Devonian time. Natural size. *B*, the siliceous skeleton of *Venus' flower basket*, Euplectella, about a foot high, living in the East Indian seas. *o*, osculum, the opening of the large central cavity (*p.c.*) now partially filled with mud. At the junction of the principal bands of spicules (*sp.b.*) were probably tufts of spicules, the bases of which have left their impressions (*sp.t.*) upon the internal mud mold. Prismodictya was probably attached to some foreign object by a flattened area at *a*. *A* modified from Hall and Clarke.

without its siliceous cap or anchoring root-tuft. After the decomposition of its soft parts, sediment very readily oozed through the meshes of the skeleton, completely filling it. Upon this sediment were impressed the form of the skeleton and the shape of its quadrate meshes. With the disappearance of the hydro-siliceous skeleton through the destructive agency of alkali-bearing percolating waters, the shape of the mass of sediment within the skeleton remained.

Prismodictya belongs to the family Dictyospongidæ (Silurian-Mississippian). These, unlike their modern representatives, Venus' flower basket, lived in comparatively shallow water. Most of the Devonian forms, as Hydnoceras, were anchored in sand or sandy muds by their root-tufts, while in the Mississippian the majority were apparently fastened to a solid object, stone or dead shell, by a more or less broadened base; this last was probably also the case with Prismodictya. Ornamental ridges may also occur (*e.g.*, Clathrospongia and Thysanodictyon), upon the outer surface as in the modern Euplectella.

Prismodictya prismatica is very abundant in the upper Devonian (Chemung) sandstones of the Appalachian region.

1. Sketch a side view of the entire specimen with a small portion in detail, noting the quadrate meshes.
2. Describe the steps in the formation of this fossil from the death of the animal to its present appearance.
3. How did the living Prismodictya differ from Venus' flower basket?

CLASS C. DESMOSPONGIÆ

Skeleton of siliceous spicules or of spongin or of both. Includes the majority of living sponges.

Order 1. Tetractinellida

Skeleton of four-rayed siliceous spicules (whence the name from Greek *tetra*, four, + *aktis*, ray, + Latin dim. *ella*). When these spicules are united with each other, it is through the addition of

spongin. These are known in the fossil state from the Cambrian to the present.

Astylospongia (Fig. 53). *Ordovician and Silurian.*

Spherical, with a shallow depression (osculum) at the summit, and with many pores (incurrent canals) over the entire outer surface. The rigid skeleton is probably due to the irregular mesh-like union of the spicules.

os.

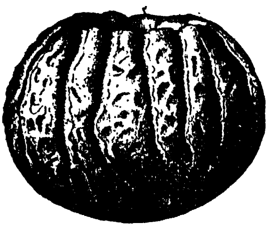


FIG. 53. — The sponge, *Astylospongia præmorsa* Goldfuss, from the Middle Silurian of Indiana (× 2). Side view showing the osculum (*os.*) above. (After Hall.)

1. Sketch the entire specimen, labeling osculum, incurrent canals.
2. How would you know this to be a sponge?

Order 2. Monactinellida

Skeleton of one-rayed siliceous spicules (whence the name from Greek *monos*, one, + *aktis*, ray, + Latin dim. *ella*). When these spicules are united with one another, it is through the addition of spongin. This order includes the few fresh-water sponges (Spongilla, etc.) and the majority of existing marine sponges; they inhabit the more moderate depths. They are known from the lower Paleozoic to the present.

The boring-sponges (**Cliona**) are compound forms with many oscula. They secrete pin-shaped siliceous spicules encased in spongin, with which, aided by a power of absorption, they bore passages in dead or living shells for protection, not for food. These sponges and boring worms help to perform the same function in the economy of nature in the sea as fungi and insects do upon land, namely the disintegration of dead organisms.

Order 3. Ceratospongida (or Keratosa)

Skeleton of horny, spongin fibers (whence the name from Greek *ceras*, horn, + *spongia*, sponge). Not definitely known in the fossil state. The common bath sponge (Euspongia) is an abundant living form.

The common commercial sponges grow in warm seas, as those of the West Indies and the Mediterranean, from tide level to a depth of 200 feet. When prepared for commerce they are torn from the sea-bottom, exposed on the hot beach to decompose, then washed in water to remove all fleshy parts, leaving the tough, fibrous, chitinous skeleton. The separate individuals of these usually compound sponges are distinguished only by the oscula; the rest of the body is intimately united with its neighbors.

Order 4. Myxospongida

Skeleton absent (whence the name from Greek *myxa,* mucus, + *spongia,* sponge). Unknown in the fossil state.

Evolution of Porifera

The first great step in the development of larger animals and a more varied fauna seems to have been the transformation of a protozoan colony of similar one-celled organisms into a single organism of many interdependent cells. In this new organism each cell must act for the best welfare of all, just as in the later evolved organism, a swarm of bees, each individual must act for the welfare of the hive. Thus, in sponges, certain cells catch and digest food, others secrete spicules, and still others are elongate and contractile, primitive muscles. There is a general law of life that, other factors being equal, the larger the organism the better its chance of survival. Thus a sponge, because of its greater size, cannot be so easily smothered by depositing sediment nor so readily eaten as is a protozoan. Sponges represent an evolution from protozoan ancestors which led to nothing beyond the sponges themselves.

The living representatives of this phylum are but rarely used for food by other animals, apparently because of the objectionable spicules and the disagreeable or poisonous excretions.

Sponges as Rock-Builders

In the Upper Jurassic of Europe (Swabia, etc.) many reefs seem to have been to a large extent formed by lime-secreting

sponges. As a rule, however, sponges were too few in number with hard parts too small in amount to have been effective rock-builders. Some siliceous concretions are doubtless due wholly or in part to the solution and redeposition of the siliceous spicules of sponges.

1. Give detailed classification of Porifera (in classes and orders).

2. Since a protozoön consists of a single cell and a sponge of many cells, why cannot the latter be considered a colony of the former?

3. What is the principal advance of the Porifera upon the Protozoa?

4. What is the characteristic skeletal element in sponges? Give variations in its chemical composition and in its structure, with examples of each.

5. Among the different sponges, give stages of the gradual replacement of spicules with spongin.

6. Describe the appearance and structure of the living commercial or bath sponge. Is it simple or compound? What is its habitat? How is it prepared for market?

7. What function did the various holes in the common bath sponge have when the animal was living?

8. Why do the boring sponges penetrate shells?

9. What is the probable origin of the phylum?

10. From the rocks of what period are the earliest records of sponges?

11. Indicate the importance of sponges as rock-builders.

CHAPTER VIII

PHYLUM III. CŒLENTERATA

The Cœlenterata are aquatic, usually marine animals, with a radial (instead of a bilateral) symmetry and with the mouth opening into the digestive cavity (cœlenteron); this latter usually forms the entire body cavity. The mouth is nearly always surrounded by *tentacles* — hollow or solid outgrowths of the body wall. A cross-section of the body wall or of a tentacle shows it to be composed of three layers, an outer layer of cells (ectoderm), an inner layer of cells (endoderm), and between these two a layer of a rather stiff structureless substance (mesoglœa) inclosing few or no cells. These animals are provided with special offensive weapons, the nettle-cells (nematocysts).

Derivation of name. — Cœlenterata > Greek *koilos*, hollow, + *enteron*, intestine. The entire cavity within the body walls acts as a digestive cavity (like the stomach and intestine of higher animals).

The Cœlenterata are divided into the following classes:

CLASS A. HYDROZOA (HYDROIDS AND MEDUSÆ)

Type of class, *Sertularia pumila* (living) (Figs. 54, 59, *C*).

This is a colonial form with the individuals — the *polyps* — in sessile cone-shaped cups (hydrothecæ) arranged in two opposite rows along a stem. The polyp consists essentially of a

hollow, sac-like digestive cavity, surrounded at the top by a single circle of tentacles, and in the midst of the tentacles an opening, the mouth. The stems, an inch to an inch and a half long, simple or branched, spring at intervals, usually in clusters, from a creeping and much-branching root-stock (hydrorhiza). This species is very abundant off the northeast coasts of North America from New Jersey to the Arctic, also on the northwest coasts of Europe. It occurs in especial profusion between tides attached to the rock weed, Fucus.

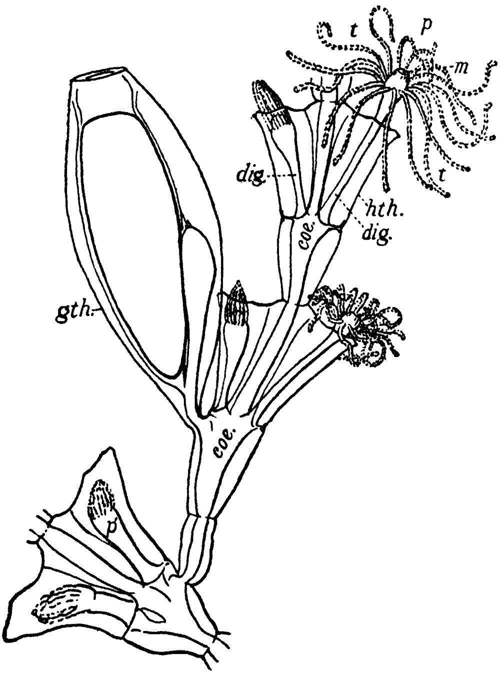


FIG. 54. — A portion of a colony of the hydroid, *Sertularia pumila*, from the coast of Massachusetts (× 60). *cœ.*, cœnosarc, — the common flesh uniting the various individuals of the colony, — through which passes the central canal; *dig.*, digestive cavity; *gth.*, gonotheca, or cup lodging a reproductive polyp; *hth.*, hydrotheca, or cup lodging a feeding polyp; *m*, mouth; *p*, a polyp expanded, in feeding position; *p'*, a polyp contracted, in protected position; *t*, tentacles.

Each polyp is continuous at its base with the central canal; its entire surface secretes a protective layer of chitin composed of superposed lamellæ. When mature it largely draws away from this protective covering. There is thus formed a cup out of which the animal can expand to get food, and into which it can withdraw for protection.

Its **food** consists of small, usually microscopic animals and plants, as well as of organic fragments. These it catches with its sixteen tentacles and by their aid pushes into its mouth. The tentacles are covered with numerous nettle-cells (nematocysts) by means of which any living prey is paralyzed and thus rendered harmless. Through the mouth, the food enters the large central or digestive cavity, into which is poured a digestive fluid secreted by some of the smaller endoderm cells lining this cavity. The food is thus digested outside the individual cells. The undigested waste is thrown out again through the mouth, while the digested food is taken up by the bordering cells through osmosis, and thus passed to all the cells, each taking what it needs for repair or growth.

Respiration is performed by the entire surface of the body, for the covering of the cells of the ectoderm (the surface layer of cells) is so thin that osmotic interchange of the excess carbon dioxide of the animal for the oxygen of the water easily takes place.

There are many **muscular** fibers, especially along the inner edge of the ectoderm, the contraction of which enables the animal to shorten its entire body and thus withdraw into its protective cup. Accompanying these muscles are large, much-branched nerve cells which regulate their action.

Reproduction is both sexual, through the development of spermatozoa and ova, and asexual, by budding. Some of the digested food passes through the base of the polyp into the central canal, and up this to the growing tip, where new buds for the formation of new polyps occur; some passes into polyps which are completely inclosed in urn-shaped cups (gonothecæ); these latter, the reproductive polyps, cannot procure their own food, but give rise to spermatozoa or ova, the union of two of which produces a new colony. Reproductive polyps are present only during the breeding season, from May to September.

Within the gonotheca develop (by budding) usually only minute jelly-fish, the medusæ; these breaking loose from the parent swim about

freely and develop spermatozoa and ova, the union of which gives rise to the sessile colony, the hydroid. This alternation of generations may be represented thus

1st Generation		2d Generation	3d Generation	
Colony	feeding polyps		males $<$ spermatozoa	
			+ - - - - - - -	New Colony
	reproductive polyps —	medusæ	females $<$ ova	

There is evidence in the order Leptolinæ that this alternation of the fixed nutritive colony with the free-swimming sexual medusa is being gradually abandoned. The medusa generation, whose special function it is to develop spermatozoa and ova, gradually becomes reduced to a few cells which, remaining attached within the gonotheca, produce the sexual products. In Tubularia the medusæ are almost fully developed, but never break loose from the parent. In *Sertularia pumila* the medusa form is entirely lost.

Sense organs. — The medusæ often have eye-spots (ocelli) at the bases of the tentacles; these are often only a few pigmented cells, but at times (as in Lizzia) a cuticular lens is present. Otocysts, too, are present upon, or near, the tentacles; these are partially open or closed pits inclosing one or more otoliths, organic or calcareous in nature, and are probably mainly balancing organs. Both ocelli and otocysts are ectodermal in origin. Like all other cœlenterates, Sertularia possesses the combined chemical sense of taste and smell.

Development. — The fertilized egg is a single cell; this splits into two cells, which in their turn divide again, and so on, until they give rise to the blastula (a single layer of cells surrounding a central cavity), and this develops by true invagination as in the sponge into the gastrula. The gastrula is vase-like in shape, with two layers of cells; between the outer (ectoderm) and the inner (endoderm) layer, and deposited by them, is a stiff gelatinous, non-cellular secretion, the mesoglœa. The ectoderm becomes ciliated, enabling the minute embryo to swim freely about. When it comes to rest, it affixes itself by root-like processes (hydrorhizæ). The opening (blastopore) of the vase-like gastrula becomes the mouth of the polyp, and a circle of outpushings around it gives rise to the tentacles. The adult is

thus practically in the gastrula stage with the body wall consisting of three layers: the ectoderm, the mesoglœa, and the endoderm, the latter lining the digestive cavity. It is of special interest that this adult animal should persist in the shape of the gastrula, since all higher animals pass through this gastrula stage very early in their development from egg to maturity. This fact is taken to mean that all higher animals have diverged from a cœlenterate ancestor in remote geological ages.

1. Examine the specimens mounted in alcohol, noting the size of a colony, its attachment, the individuals, each with its circle of arms surrounding the mouth.
2. Sketch, from the slide under the compound microscope, one individual animal and its connection with the central canal of the colony. Label tentacles, mouth, cup, central canal.
3. Indicate the portion of an animal capable of being preserved in the fossil state.
4. How does the animal capture its food?
5. What prevents a large, active animal swallowed by the polyp from struggling and thus tearing the soft body walls to shreds?
6. How is the food digested? How assimilated?
7. How does the digestion of food differ from that in sponges and protozoöns?
8. How does the polyp breathe?
9. What kind of a muscular and nervous system does it possess?
10. How does it multiply?
11. Trace the development of an individual from the fertilized egg to adulthood.
12. Describe the blastula, the gastrula.
13. What are medusæ?
14. Why is a colony of Sertularia, which has a plant-like attachment to foreign objects, placed with the animals?

General Survey of Class Hydrozoa

Aquatic animals with the body consisting of a large, centrally placed, digestive cavity with but one opening (the mouth); this mouth is usually surrounded by many arms (tentacles).

These are lowly forms of animal life with the cells making up the body arranged in two layers, the ectoderm and endoderm,

separated by a non-cellular layer, the mesoglœa. The endoderm lines the large, undivided digestive cavity.

Hydrozoöns are abundant from the Ordovician to the present.

Derivation. — Hydrozoa > Greek *hydor*, water, + *zoon*, animal.

Classification of the Hydrozoa. — With the exception of the orders Siphonophora (*e.g.*, Physalia), Hydrocorallinæ, and Stromatoporoidea, there is no generally accepted classification. Some authors divide the remainder into four orders based entirely upon the medusa, others into two orders based upon the fixation of one generation (the Leptolinæ or hydroids) or non-fixation (the Trachylinæ). According to this latter classification, the genera Sertularia, Hydra, and Hydractinia belong under the fixed order.

Order Hydrocorallinæ

Colonial Hydrozoa, the common base of the colony secreting a massive calcareous support not unlike some coral masses. This consists of a network of calcareous fibers and is traversed by tubes which lodge the polyps. The tubes are of two sizes; the larger (gastropores) lodge the feeding polyps and the smaller (dactylopores) lodge the protecting polyps Both sets of tubes are divided in the older part by horizontal partitions or tabulæ. Millepora and Stylaster are living genera.



FIG. 55. — The Staghorn coral, Millepora, from the Florida coasts.

Millepora (Figs. 55, 56).

Eocene to present.

Encrusting or branching masses with a structure as noted above. The beautiful staghorn coral (*Millepora alcicornis*) occurs off the Florida coasts.

Sketch surface view and vertical section. Label gastropores, dactylopores, and tabulæ.

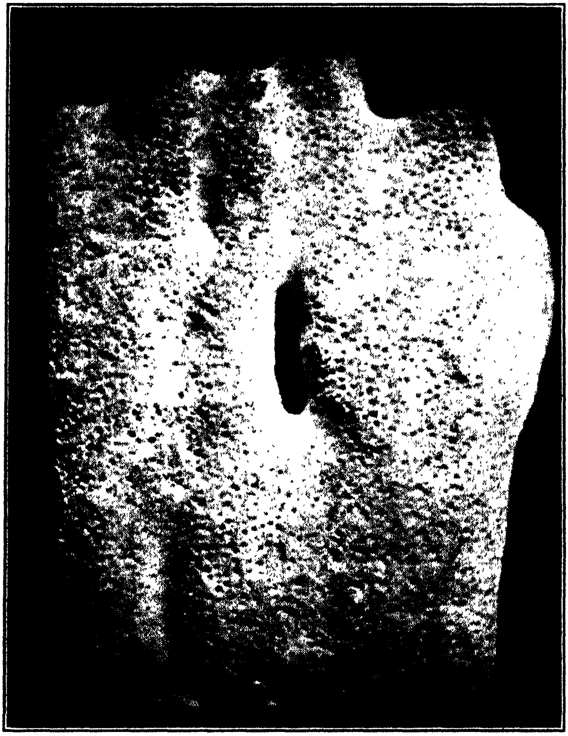


FIG. 56. — Portion of Figure 55 enlarged. All the pores seen by the unaided eye are gastropores.

Order Stromatoporoidea

Spreading to subglobular calcareous masses which sometimes attain a diameter of several feet (Figs. 57, 58). They are composed of numerous concentric laminæ, separated by interspaces and supported by radial pillars. The apertures for the emission of polyps are situated on the upper surface of the laminæ. The genera Clathrodictyon and Stromatopora are abundant in the Silurian and Devonian of North America.

They are confined to the Paleozoic, where they constitute at times whole beds of limestone. They are thought by many

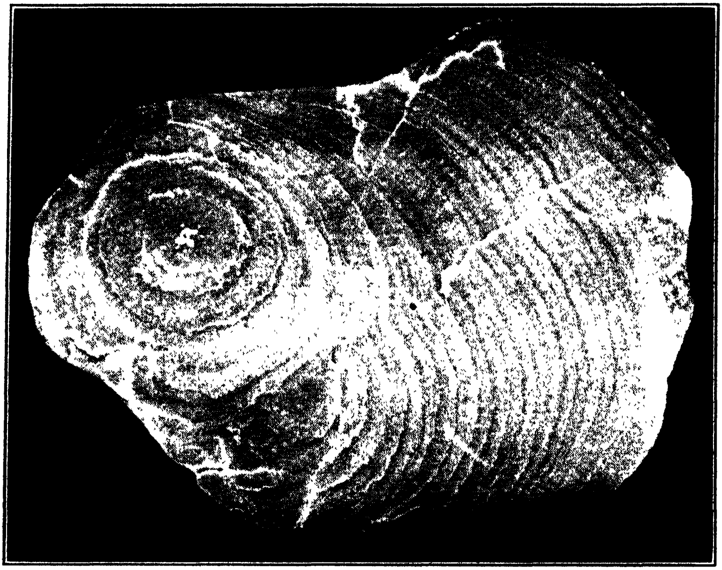


FIG. 57. — Polished section of a Stromatopora head (× ½) from the Hamilton of Michigan.

to be related to Hydractinia and Millepora; by others they are considered to be sponges.

1. Sketch a section across the laminæ of any genus. Label laminæ and radial pillars.
2. Where were the polyps situated?
3. To what era are the stromatoporoids confined?

Order Siphonophora

Colonial, pelagic Hydrozoa, with remarkable diversity of form among the various individuals in a colony. They are often supported by a float (pneumatocyst) of their own manufacture. Not known in the fossil state. Example, Portuguese man-of-war (Physalia).



Fig. 58. — Portion of Figure 57 enlarged.

CLASS B. GRAPTOZOA (GRAPTOLITES)

Type of class, *Diplograptus foliaceus* (fossil) (Fig. 59).

This species is like the hydrozoön, Sertularia, in being colonial. It consists of two crowded rows of cups (hydrothecæ) like saw teeth, arranged in opposite series along a stalk to which they are broadly but obliquely fastened. Each cup, a subprismatic tube longer than wide, represents as in Sertularia one individual polyp; in it were lodged the soft parts and into it the entire polyp could withdraw for protection. At its base it was connected by means of a tube with the central canal running the length of the stalk. Unlike Sertularia, however, it was not attached to the sea-bottom in shallow water, but floated freely at its surface suspended from a float-like disk (Fig. 59, *fl.*), somewhat like forms included with the hydrozoan order Siphonophora.

As in Sertularia, the protective covering was of chitin, but

its partial decomposition, due to its great age, aided probably by the heat engendered by pressure of the overlying sediments, has resulted in driving off most of the hydrogen, oxygen, and

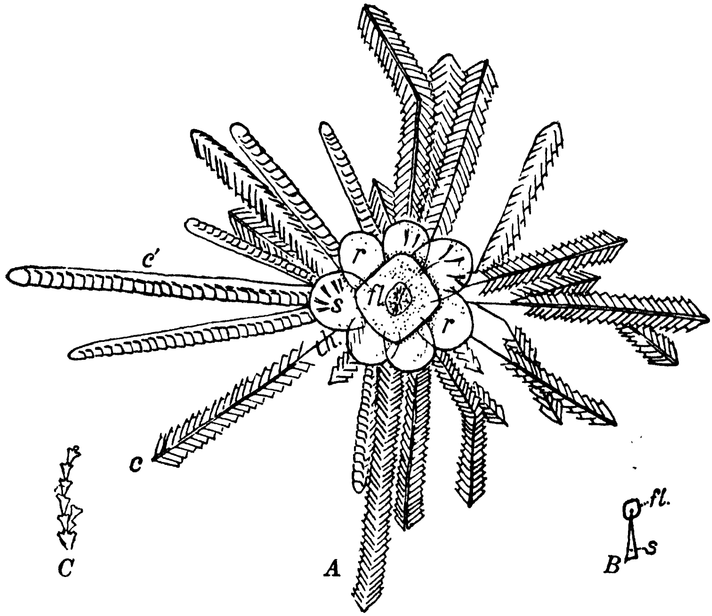


FIG. 59. — *Diplograptus foliaceus* Murchison, from the Utica (Ordovician) shale of New York. *A*, a compound colony of graptolites. Natural size. *B*, a young graptolite just emerged from the reproductive bladder (*r*). Natural size. *C*, the living hydrozoön, *Sertularia pumila* (× 2), for comparison of external forms. *fl.*, the supporting float-like disk; *r*, reproductive bladders in three of which are young graptolites (siculæ, *s*); *th.*, thread supporting the colonies (*c*, *c'*); *c*, side view of colony showing the two rows of cups; *c'*, front view showing the width of the cups. *A*, *B*, slightly modified from Ruedemann.

nitrogen, thus leaving as fossil only a film composed mostly of carbon.

It was very probably similar to Sertularia in the character of its food, its digestive, excretory, and nervous systems, and in its assimilation and respiration.

Its reproduction was likewise both sexual and asexual, and

it seems to have lacked the jelly-fish stage. The union of a spermatozoön and ovum gave rise to the first polyp which secreted the earlier protective cup, called the sicula. From this by budding developed the colony (rhabdosome).

In the genus Diplograptus (Ordovician-Silurian) the cups (hydrothecæ) are arranged in two rows along the stem (whence the name from Greek *diploos*, double). In a side view, the virgula shows as a raised ridge running through the middle of the colony, while each cup has a thick outer edge owing to the compression of its entire width.

D. foliaceus is abundant in the Chazy to Utica (mid-Ordovician) shales of North America and in beds of similar age of Europe and Australia.

1. Sketch a portion of the colony, enlarging it three times. Label cup, virgula, sicula (if present).
2. In life what part of the animal was probably visible outside the cup when feeding?
3. Give in tabular form resemblances to and differences from Sertularia.
4. What is the chemical composition of the fossil? What produced this change from its composition when living?

General Survey of Class Graptozoa

Extinct, colonial cœlenterates, fixed to some object upon the sea-bottom, or floating upon the surface attached to drifting seaweed or to a pneumatocyst of their own manufacture. They secreted a protecting and supporting skeleton of chitin, with the separate individuals lodged in pits upon, or cups along the margin of, the chitinous stalks.

These animals are known only from their colonial phase, the presence of the jelly-fish phase not yet having been demonstrated. Some forms, at least, as Diplograptus, developed direct, without the alternate generation; here generative cysts formed on the colony, in which developed the siculæ (embryonic graptolites), which were scattered upon the rupture of these cysts and grew into new colonies.

Habitat. — Graptolites, with the exception of some of those belonging to the order Dendroidea, lived suspended. That they did not live fastened to the sea-bottom is shown by the fact that their remains are always confined to one bedding plane, never passing vertically from one bed to another. They are always spread flat as though they had fallen with the entombing sediment. While they are found in all kinds of sediment, including limestones, they are most numerous in very fine-grained, carbonaceous shales. The carbon of the shales was probably derived from floating marine plants, not from the abundant graptolite remains, for seldom, if ever, do decomposed rhabdosomes pass into the surrounding shales. Since it is probable that few land plants existed during Ordovician times — the climax of graptolite development — it is likely that the carbon is due to the partial decay of marine plants. Many fragments of seaweed occur in such typical graptolite beds as the Utica shale of the Ordovician of the Appalachian region. Suspended from these plants were representatives of the Axonolipa division of the Graptoloidea, while floating among them were Axonophora colonies supported by their pneumatophores. The latter probably sank during periods of roughened seas, as some of them had developed ridges which might have subserved such a directive function. A roughening of the water surface would cause a rain of the broken, fragile colonies upon the sediment beneath.

This method of growth accounts likewise for the wide distribution of so very many of the species. That even the Graptoloidea order was derived from forms which grew upright upon the sea-bottom as did many of the Dendroidea is suggested by the reversion of direction of the cups in a colony, the embryonic cup or sicula growing in a direction opposite to that of the rest of the cups.

Graptolites were abundant during the Ordovician and the Silurian, while a few stragglers continued to exist into the Mississippian. They occur mostly as flattened carbonized films on shale.

Relation of the Graptozoa to other classes. — Graptolites differ from hydrozoöns in the presence of the sicula, the virgula, and, in some species, paired muscle impressions. The sicula is very similar to the primordial polyp of the alcyonarian coral Pennatula, which persists in the colony as the stalk, and which, like the sicula, projects below the first lateral polyps. In Pennatula (sea-pen) the colony is supported by an unbranched horny axis, with one end embedded in the mud at the sea-bottom, while the opposite end bears the polyps on lateral branches. This horny axis, as well as that of Gorgonia, resembles the virgula of the graptolites. A resemblance to bryozoöns is seen in the division of the graptolite sicula into two parts. The graptolite cup and sicula exhibit a bilateral symmetry as do, faintly, the cups of corals and many other cœlenterates. The hydrotheca is a distinctly hydrozoön structure. The same is true of the pneumatophore, as seen in the Siphonophora. The division of the sicula and the presence of muscles do not outweigh the other cœlenterate characters. The group seems best placed as intermediate between the Hydrozoa and the Anthozoa. The muscles, probably used either to withdraw the polyp into its cup or to close the opening of the flexible hydrotheca, represent the evolution of a structure in advance of that usual for the phylum. Such an evolution is seen frequently in fossil groups and renders difficult their placement in existing classes and phyla.

Derivation. — Graptozoa > Greek *graptos*, written, + *zoön*, animal. The resemblance of these fossils, especially those of the order Graptoloidea, to the ancient writings on stone suggested not only the name of the order but also the latter part (graptus) of most of the generic names of graptolites.

The graptolites are subdivided as follows:

Order 1. Dendroidea

Colony (rhabdosome) branching irregularly in a funnel or fan-like manner. Cups (hydrothecæ) usually pits upon the branches.

Probably most of the Dendroidea, especially the heavier and more shrub-like forms, were sessile in an upright position, attached to some object at the sea-bottom; this would likewise account for their local distribution. Some have adhesive threads (hydrorhizæ), like Sertularia and other modern sessile hydroids. Many of the species of Dictyonema, on the other hand, have a very wide distribution, and, at least in their younger stages, floated about attached to a supporting disk.

The name is from the tree-like (Greek *dendron*, a tree) method of growth of the colony.

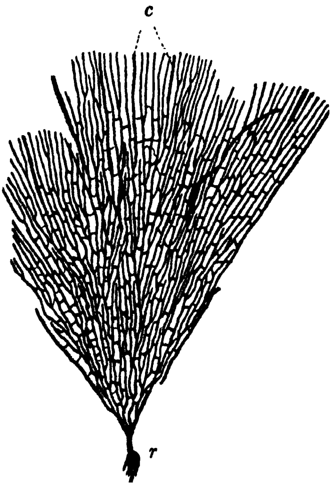


FIG. 60. — *Dictyonema flabelliforme* Eichwald, from the lowest Ordovician of New Brunswick, showing cups (*c*) and roots (*r*). Natural size. (After Matthew.)

Dictyonema (Fig. 60).

Ordovician-Mississippian.

Colony (rhabdosome), a rapidly expanding fan or cone with cups upon the inside. The slender branches are united at short intervals, producing a net-like appearance (whence the name from the Greek *dictyon*, net, + *nema*, thread). When young, the rhabdosome was suspended from a long, thin thread attached to a chitinous disk; later (at least at times), it was sessile by rootlets. *D. flabelliforme* is common in the earliest Ordovician rocks of eastern North America and Europe.

1. Sketch the fossil; if the entire colony is not preserved, dot in its probable shape and size.
2. Where upon the colony did the individual animals live?
3. What probable difference between the habitat of the young and of the adult? Reasons.
4. What is the significance of the name?

Order 2. Graptoloidea

Colony (rhabdosome) simple, or if branched it is not tree-like. Cups (hydrothecæ) usually distinctly marked and projecting. The Graptoloidea lived suspended, floating.

This order embraces two divisions:

1. Axonolipa. — Virgula absent. Representatives of this division were suspended from seaweeds. Named from the Greek *axon*, axis, + *lipein*, to lack, referring to the absence of the virgula.

Phyllograptus (Fig. 61). *Ordovician.*

Colony consisting of four short, broad, leaf-like (whence the name from Greek *phyllon*, leaf) branches grown together, each pair back to back, in such a way as to form a cross in section. Hydrothecæ upon the outer edge of each branch.

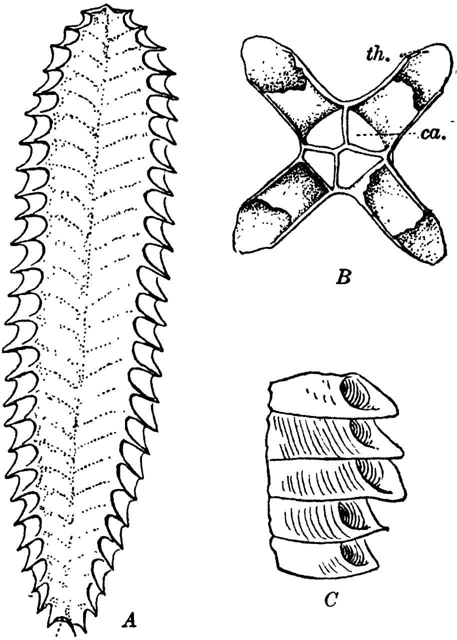


Fig. 61. — *Phyllograptus angustifolius* Hall, from the Ordovician of New York. *A*, entire colony (× 4), showing the earliest cup, the sicula (*s*); the opening of the latter is between the two spines. *B*, transverse section through the colony (× 6); *ca.*, common canal with its four longitudinal septa; *th.*, the individual cups (thecæ). *C*, *P. ilicifolius* Hall (× 8), showing the openings of five cups, in each of which was lodged the soft body of a single individual. (All redrawn from Ruedemann; *A* and *B* after Holm.)

1. Sketch the entire colony, labeling the cups.
2. Make an ideal cross-section through the colony.

2. Axonophora. — Colony with a median axis, or supporting rod of chitin, called the virgula, running its entire length.

The division Axonolipa is replaced from the mid-Ordovician onward by the Axonophora, *i.e.*, those with an axis (virgula). This axis of chitin is brittle, which probably accounts for the fragmentary condition of most of these species. The virgula extends through the entire colony (rhabdosome), even penetrating the sicula. Probably all of the Axonophora were attached to a float of their own secretion. Examples are Diplograptus, Climacograptus, and Monograptus.

Named from the presence of the virgula, from the Greek *axon*, axis, + *pherein*, to bear.



FIG. 62. — The graptolite, *Climacograptus typicalis* Hall (× 7), from the Utica shale of New York. Only the end of the colony bearing the sicula (*s*) is here shown. (From Ruedemann.)

Climacograptus (Fig. 62). *Ordovician.*

Hydrothecæ sharply curved below, the upper edge or aperture more or less horizontal; hence they are widely separated. The colony thus presents a ladder-like appearance (whence the name from the Greek *climax*, a ladder). The straight outer margins of the hydrothecæ are parallel to the axis of the colony. *C. typicalis* is very abundant in the Utica (Ordovician) shales of New York State.

1. Sketch a portion of a colony, indicating a hydrotheca and its aperture.
2. What is the chemical composition of the fossil at present? When living?
3. How do you account for the great abundance and the fragmentary condition of these colonies, as for example in the Utica shale?

Monograptus (Fig. 63). *Silurian.*

Cups (hydrothecæ) arranged in one row along the straight or curved stem (whence the name from the Greek *monos*, one). The virgula can be seen as a ridge extending the length of the colony opposite the cups. *M. clintonensis* is an abundant and

well-preserved species in the Silurian (Clinton) shales of New York State.

1. Sketch portion of a colony, enlarging it three times. Label a hydrotheca and its aperture, the virgula, the position of the central canal.
2. Sketch the probable appearance of the soft body of a polyp with tentacles expanded.
3. Briefly describe the probable digestive system of Monograptus.
4. How was the hydrotheca formed?
5. What use did this cup subserve?
6. What is the significance of the name Monograptus?
7. Give reasons for placing this under the Cœlenterata rather than under the Porifera.

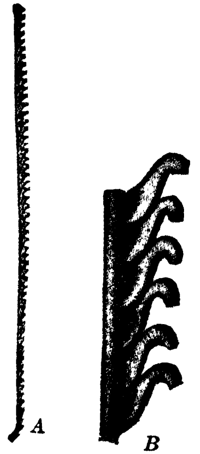


FIG. 63. — The graptolite, *Monograptus clintonensis* Hall, from the Clinton formation (Middle Silurian) of New York. Side views. *A*, natural size (from Hall); *B*, an enlargement of six cups. (From Ruedemann.)

CLASS C. SCYPHOZOA (JELLY-FISH)

Large, free-swimming, umbrella-shaped jelly-fish (medusæ). The margin of the umbrella is usually lobed, bearing tentacles, while the mouth occupies the position of the umbrella's handle. They develop directly from the egg or by the alternation of a sessile stage; in the latter case they multiply by transverse fission. They swim by rhythmically opening and closing their umbrella-like bodies. Their food consists of small fish, crustaceans, and even of each other. None live longer than a year.

The Scyphozoa are known to have existed from the Cambrian (Fig. 64) to the present. They are entirely without hard parts and consist of about 99 per cent water, so that only under exceptional conditions have they left a record of their presence. At times in very fine-grained muds, as in the lithographic limestone of Bavaria (of Upper Jurassic age), and in the Middle Cambrian Burgess shales of British Columbia, impressions of

their soft bodies are preserved, or even imprints of their tentacles trailing over the yielding mud. At other times the lobed digestive cavity has become filled with fine sand or mud; this filling in turn becoming covered by other mud before the soft

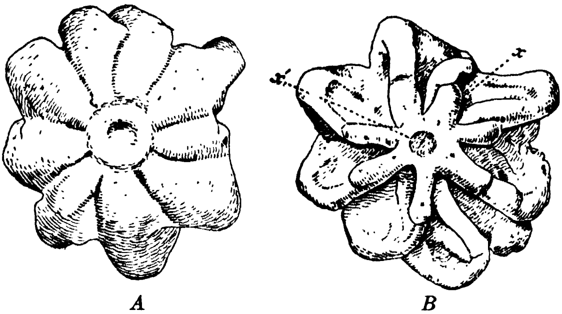


FIG. 64. — A fossil jelly-fish, *Brooksella alternata* Walcott, from the Middle Cambrian of Coosa Valley, Alabama. *A*, top view showing the nine lobes and a trace of the furrow in the ring about the central disk; *B*, under view of same specimen. The lobes are shown, as also are what appear to be oval arms (x) for carrying food to the central stomach. A central depression (x') may represent the position of the mouth. Natural size. (After Walcott.)

jelly-fish body has become disintegrated, preserves the outline of its containing cavity (Fig. 64).

Derivation. — Scyphozoa > Greek *scyphos*, cup, + *zoon*, animal, referring probably to the inverted cup-like appearance of the swimming jelly-fish.

CLASS D. ANTHOZOA (CORALS)

Type of class, *Astrangia danæ* (living) (Fig. 65).

This is a colonial form, with the individuals, the polyps, in sessile, star-like cups encrusting stones, dead shells, etc. Living and active it looks much like a tuft of white, translucent moss; after death and the decomposition of the flesh nothing is seen but a calcium carbonate mass (one-half to three inches in diameter) of star-like cups (corallites), each with a diameter of three to five millimeters.

It lives in shallow seas off the coast of North America from Florida to Cape Cod; it does not occur in the colder water north of the Cape.

Each *polyp*, glassy white and translucent in appearance, consists of a barrel-shaped body, averaging 3 mm. wide by 9 mm. high when fully expanded, with a circle of 18 to 24 long, tapering tentacles surrounding the top. At the center of the top and slightly raised is the oval mouth; this leads through a short

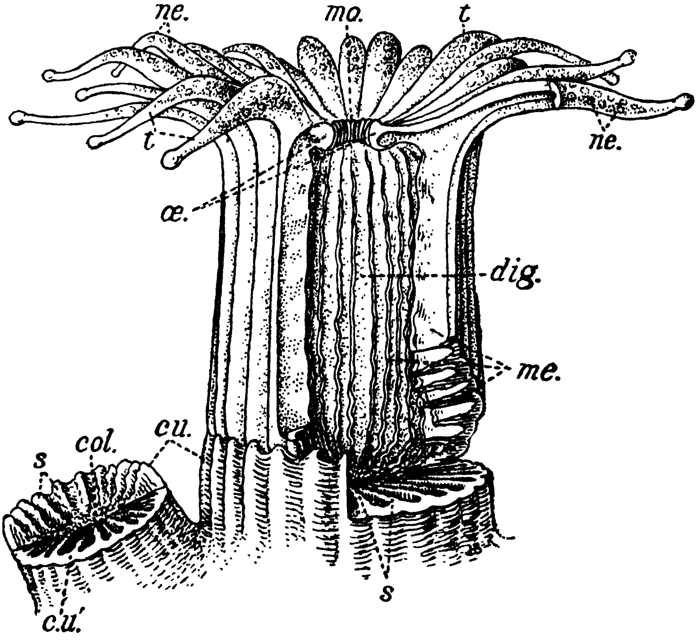


FIG. 65. — The common coral, *Astrangia danæ* (× 12), from Long Island Sound, showing a polyp in feeding position upon the calcareous, cuplike base (*cu.*), also (at left) the coral portion of a bud without its secreting polyp. *col.*, the spongy pseudo-columella; *cu.*, the cuplike calcareous base secreted by the polyp; *cu′.*, part of the cup sectioned transversely; *dig.*, digestive cavity, — the entire interior of the barrel-shaped body; *me.*, mesenteries; *mo.*, mouth; *ne.*, clusters of nettle-cells, by means of the poison in which the prey is paralyzed; *œ.*, œsophagus; *s*, septa (which alternate with the mesenteries); *t*, tentacles (one is partly dissected to show that its hollow interior is continuous with the large digestive cavity of the polyp).

œsophagus into the large digestive cavity. The digestive cavity constitutes the entire interior of the body, but is partly divided into compartments by radial partitions (*mesenteries*, Fig. 65, *me.*); each intermesenteric compartment is continuous with a hollow tentacle.

The polyp **preys** upon marine animals — small crustaceans, worms, etc. These it catches with its tentacles. Each tentacle ends in a white knob and is speckled all over with white warts, each one of which is a cluster of nettle-cells (nematocysts). When one of these cells is touched it sends out a long barbed, thread-like tube, through which poison is forced. This multitude of nettle-cells, piercing the prey, paralyzes it. The tentacles then push this food into the mouth, through which it enters the digestive cavity. The white cords (mesenteric filaments) edging the mesenteries are crowded with nettle-cells; these cords, wrapping themselves about the prey, complete the killing, while the many gland cells covering the cords pour out a digestive fluid.

After the digestion of the food, the waste is thrown out through the mouth; the digested portion mingled with the sea water is forced by the contractions of the body through the radial compartments and into the tentacles, the various cells taking what they need for growth and repair. The entire body acts thus as a huge blood-vessel, and since the digestive cavity connects freely through the mouth with the water of the ocean, the "blood" consists of sea water mingled with nutritive portions of food.

Respiration is performed mainly by the tentacles; these being thin and containing the body fluid or blood, permit a free interchange of the excess waste carbon dioxide, etc., of the body for the free oxygen in the sea water.

Well-developed **muscles** are present. There is a sphincter muscle surrounding the body at the top which draws in the tentacles and closes the mouth much as a string may close a bag by gathering it together. Muscular layers line the mesenteries on each side, and it is through their expansion and contraction,

thus admitting and expelling water, that the animal is able to expand and contract. When the animal is disturbed, these muscles contract, the tentacles are rolled inward, and the entire body becomes a small dome-like mass.

There are no **sense organs** present, excepting specialized tactile cells, and a well-developed chemical sense, taste-smell. There are nerves present in both ectoderm and endoderm which regulate the complexity of the animal's movements.

Astrangia **reproduces** by development of spermatozoa and ova. The sexes are distinct. The reproductive elements form by the division of some of the endoderm cells of the mesenteries near the lower end of the body. The product of the union of an ovum and spermatozoön develops rapidly into an ovoid, hollow body, the planula (blastula stage). This elongate body has two layers of cells, an inner (endoderm) and an outer ciliated layer (ectoderm). After swimming about for a time by means of its cilia, the planula settles down to the bottom of the water and becomes attached. At the free end an inbending of the wall occurs, forming mouth and œsophagus and finally piercing the inner cavity (gastric cavity).

Secretion of lime. — After the larva sinks down from its free-swimming condition and rests upon some object, certain ectoderm cells (calicoblasts) of the base of the animal begin to secrete a calcareous liquid directly exterior to themselves, and from this is inorganically crystallized the *calcium carbonate* (Fig. 66). According to some students the "calcareous deposit is laid down within the individual calicoblasts of the ectoderm. At the same time new ectodermal cells are formed next the mesoglœa, and these which are undergoing calcification become loose external layers of partly calcareous, partly organic tissue." Ogilvie.

This deposit, developed between the base of the animal and the rock or other foreign object to which it is attached, gradually forms a calcium carbonate base (called the *basal plate*) outlining the size and shape of the base of the soft parts of the animal. At the same time the soft basal portion between the

mesenteries bends upward, permitting a greater deposit of lime here; since the mesenteries radiate from the center to the edge of the soft body portion, these ridges (*septa*) of calcium carbonate radiate likewise. These septal ridges grow higher and higher, resulting finally in the thin septa, over each of which are folded the three layers — ectoderm, mesoglœa, and endoderm. The upper edges of the septa are conspicuously toothed, giving them a saw-like appearance. The septa are seen to alternate with the mesenteries but are external to the polyp, *i.e.*, each

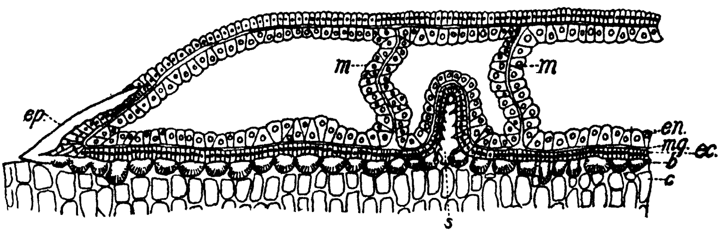


FIG. 66. — Vertical section through the edge of a very young stage of the coral, *Astroides calicularis*, which has fixed itself to a piece of cork (*c*). Very much enlarged. The deposits of lime (*b*, *ep.*) are apparently thrown down outside the ectoderm (*ec.*) but through the agency of these cells. *b*, basal plate; *ec.*, ectoderm; *en.*, endoderm; *ep.*, epitheca; *mg.*, mesoglœa; *m*, mesentery; *s*, septum, developed by upward bending of wall of animal between the mesenteries (*m–m*) upon the basal plate (*b*). (Redrawn from Lankester's Zoölogy, after Von Koch.)

septum corresponds to a radial inpushing of the base and lower sides of the polyp. The outer portion of the barrel-shaped body of the animal early bends upward faster than the inner portion; it thus results that the non-porous deposit of lime thrown down by the ectoderm takes on a cup-like appearance, called the *calyx*, with the septa extending from the edge of the cup down to its center. Later the longest septa, expanding, unite with one another to form a spongy, central mass, the *pseudo-columella*.

As the animal grows in circumference and adds new mesenteries, and new tentacles, so the calcareous base increases in circumference and new septa develop between the older ones —

six in the first set, six in the second, twelve in the third. The animal thus impresses its growth stages from youth to maturity upon its coral secretion, and accordingly we would look towards the narrower end of the coral for the record of its youth.

The basal portion of the polyp grows a very short distance from the edge of the cup out over the shell or stone upon which it is fastened; from this basal expansion bud up new polyps, while from their basal expansions or from that uniting them with their parent or each other, arise other buds. All these finally develop into polyps capable of catching and digesting their own food; but until then, they grow through the nourishment contributed by all the other polyps, for the digestive cavities of all the colony are continuous with one another through these basal expansions — the common flesh, or *cœnosarc.*

1. Examine Astrangia, noting the tentacles, mouth, œsophagus, mesenteries, and their relation to the septa, digestive cavity, nettle-cells.

2. Examine the sea anemone: (*a*) an entire specimen; (*b*) an individual sectioned vertically through the mouth. Note tentacles, mouth, œsophagus, mesenteries.

3. What is the habitat of Astrangia?

4. Of what does its food consist? How does it procure it?

5. What keeps the prey from struggling after being swallowed, and thus injuring the soft body of its captor?

6. Briefly describe the digestion of the food, excretion of the waste, and the method by which the nourishment reaches all parts of the body.

7. How does Astrangia breathe?

8. What muscles are present? Their use?

9. What is the function of the nerves?

10. What sense organs does it possess?

11. Describe the development of Astrangia from the egg to adulthood, noting quite fully the development of the hard parts.

12. What record of this development is present in the coral secretion of an adult?

13. How does a single polyp become a colony?

General Survey of Class Anthozoa

Usually sessile polyps which differ from Hydrozoa in the possession of a short œsophagus, differentiated from the digestive

cavity, and in the division of the body chamber into radiating compartments by means of the mesenteries.

Some Anthozoa, as the sea anemone, are without hard parts, but in most forms a skeleton of lime or chitin is secreted by the ectoderm, more rarely by the mesoglœa. The simplest form of coral skeleton is that composed of microscopic spicules of lime carbonate of different shapes, developed in great quantities in the mesoglœa and remaining detached, as in Alcyonium (" dead men's fingers "). In some forms the spicules are firmly cemented together, thus forming tubes (" organ-pipe coral," Tubipora) or a branching axis (" precious red coral," Corallium). In most corals there are no spicules present but a calcareous skeleton is secreted by the outer surface of the ectoderm of the lower part of the polyp. This entire skeleton is called the *corallum;* when consisting of one individual it is called simple; when of many, it is termed compound. In the latter case each individual is termed a *corallite.* In a simple coral, or a corallite, the outer wall (*theca*) bounds the radiating vertical plates (*septa*). The depression in the broad end of the coral, called the *calyx,* was occupied by the base of the polyp and into this it could partly withdraw for protection. In many corals the theca is surrounded by another calcareous layer with ring-like wrinkles, the *epitheca;* this was secreted by the external surface of the ectoderm at the base of the polyp. In some forms the partial or complete absence of one of the principal septa caused the formation of a groove or *fossula;* it has been suggested that the mesenteries bounding this produced most of the reproductive elements. For the formation of the septa and basal plate see page 165. Projecting upward from the base at the center of the coral is often a little column, the *columella;* this is secreted by the center of the base of the polyp; the ectoderm bends upward just as in the formation of septa, except that it is domed up instead of being ridged up. In the interior of a coral there are usually present besides the septa, tabulæ, and dissepiments. *Tabulæ* are the transverse partitions extending across the entire space within a coral from wall to wall, secreted by the ectoderm

of the base of the polyp like successive basal plates. As the sides of the theca in some species grow higher the polyp cannot occupy the entire interior and hence draws itself upwards, and wherever it rests for a time a tabula is built beneath it. These periods of quiescence may follow the expenditure of energy at times of reproduction, either sexual or asexual. *Dissepiments* are the horizontal or oblique plates connecting adjoining septa, formed in a manner similar to tabulæ, except that the base of the polyp is withdrawn in sections, not as a distinct whole, nor at such regular intervals.

The *nettle-cells* (nematocysts) contain barbed threads (some about one-fortieth of an inch long) which can pierce by their sudden unrolling a man's calloused foot; millions occur on the tentacles. Each one is used but once, but new ones are continually being formed. The polyp can reproduce lost parts and a small piece of the base can reproduce the whole animal.

Reproduction is sexual or asexual. In *sexual* reproduction the reproductive elements are formed in the endoderm of the mesenteries; there is no medusa stage. The new animal resulting from this method of reproduction is a single individual.

In *asexual* reproduction the process of budding or of division forms from this single individual a colony of various shapes and often of great size. In the Alcyonaria buds are always formed on tubular outgrowths of the polyps, the *solenia*, never directly from the polyps (*e.g.*, Tubipora, Syringopora). In the Zoantharia buds arise directly from the polyp or from the cœnosarc. Except for a few forms, this subclass (Zoantharia) is divided into the perforate and the imperforate orders. In the *perforate corals* (as Acropora) the spongy tissue (cœnenchyme) is perforated by many canals permanently connecting the digestive cavities of all the polyps of the colony. In the *imperforate corals* (as Astrangia) the canals do not penetrate the cœnenchyme, but connect the polyps over the edge of the calices.

In the Zoantharia, asexual reproduction takes place also by equal or unequal division; that is, the polyp divides into two or more individuals, each taking a portion of the mouth and some

of the tentacles, mesenteries, etc. This division usually takes place by the sides of the mouth growing inward, thus gradually constricting the original mouth. There thus result two mouths in place of one, each surrounded by its own circle of tentacles. Usually the digestive cavity also divides completely so that in each separate polyp the mesenteries and consequently the septa radiate in all directions from a separate center. The incomplete division is illustrated by the "brain-coral" (Meandrina); in this the mouth divides completely but not the digestive cavity and consequently not the calyx; a repetition of such division gives rise to the long, calcareous furrows, characteristic of Meandrina, each surmounted by many polyp mouths.

Some living sea anemones are known to be at least seventy years old; other species live for a year only. In the lime-secreting compound corals, there would seem to be no reason why the individual which started the colony should not continue to live as long as the physical conditions permit the colony to exist.

Distribution takes place mainly in the larval stage when the animal is free-swimming. All forms are marine. They occur from sea-level to a depth of three and one-fourth miles, and therefore at all temperatures. The deep-sea corals are solitary forms. Compound corals are very abundant on coral-reefs. The conditions for the reef-building corals are that the temperature be not lower than about 68° F., the water usually not deeper than 200 feet, and that there be but little sediment in the water.

In the formation of coral-reefs corals enter to a much less degree than was formerly supposed; in at least many reefs lime-secreting plants are the chief agent. (See p. 61.)

Anthozoa are known from the Cambrian to the present.

Derivation of name. — Anthozoa > Greek *anthos*, flower, + *zoon*, animal; in reference to the flower-like appearance of the expanded polyp, especially of the more brilliantly colored tropical species, the tentacles corresponding to the petals, and the region about the mouth to the disk.

The Anthozoa are subdivided into the following subclasses and superorders:

SUBCLASS 1. ZOANTHARIA

Tentacles are usually hollow and simple, never pinnate; they are four to six, or more than eight in number, with a usually equal number of mesenteries and septa.

Skeleton present or absent; when present it is developed by the ectoderm and may be horny or calcareous, but is never in the form of scattered spicules.

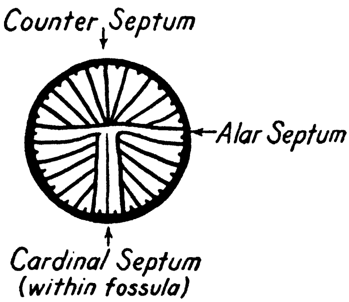


Fig. 67.—Cross section of *Streptelasma profundum* (Owen) from the Middle Ordovician of eastern North America.

Superorder A. Tetracoralla

Simple or composite corals with septa in quadrants (whence the name from Greek *tetra-*, four). (Fig. 67.) Corallum calcareous. Entirely extinct, known from the Ordovician to the Permian.

Microcyclas (Fig. 68). *Devonian.*

Simple, disk-shaped (whence the name from Greek *mikros*, small, + *cyclos*, circle). It consists merely of a calcareous plate with ridge-like septa and a fossula in the position of the cardinal septum. (Hadrophyllum may be used in place of Microcyclas, though this has three fossulæ, that of the cardinal septum being the largest.)

1. Sketch a specimen, top view, noting septa, fossula.
2. How was the calcareous plate secreted? the septa?
3. Sketch the polyp in place upon the calcareous base.
4. What is possibly the origin of the fossula?

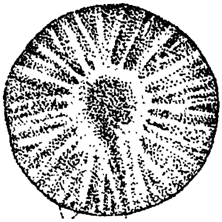


FIG. 68. — A simple coral, *Microcyclas discus* Meek and Worthen, from the Hamilton (Middle Devonian) of Illinois. *fos.*, fossula; *sep.*, septum. Natural size. (Redrawn from Meek and Worthen.)

Heliophyllum (Figs. 6, 69). *Devonian.*

Coral usually a single cup, not compound; septa numerous, slightly twisted near center of coral and thickened on their sides by conspicuous vertical ridges (carinæ). (Name from Greek *helios*, sun, + *phyllon*, leaf (coral) because of the septa radiating conspicuously like the rays of the sun.)

H. halli from the Hamilton formation of eastern North America is one of the most abundant American species; in this as in all true Heliophyllums, carinæ are lacking for some distance from the apex of the cup, and then appear only gradually. It thus in its individual development passes through a stage in which in this respect it is similar to Streptelasma, a Tetracorolla coral ranging from the Ordovician to the Devonian.

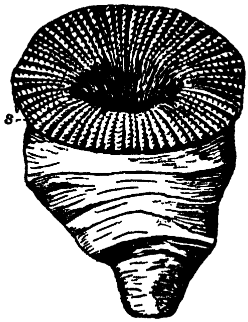


FIG. 69. — The coral *Heliophyllum halli* E. and H. from the Hamilton (Middle Devonian) formation of New York. This limestone mass was deposited by a single individual, as can be told by the septa (*s*) radiating from a center. The flesh of the animal rested upon this mass and within the central, cuplike cavity; it covered only the upper portion. Natural size. (From Hall.)

1. Sketch (*a*) view of entire specimen, showing both side and top, (*b*) horizontal section near top, (*c*) horizontal section near tip. Note septa, carinæ, dissepiments.
2. How were the septa formed? the carinæ? the dissepiments?
3. What does the section 1 *c* suggest as to the ancestry of Heliophyllum?

Columnaria (Fig. 70). *Ordovician to Devonian.*

This is a closely compound coral with prism-shaped corallites (whence the name from Latin *columnarius*, formed of columns). The corallites are thick-walled with well-developed tabulæ. The polyp occupied only the space above the last-formed tabula.

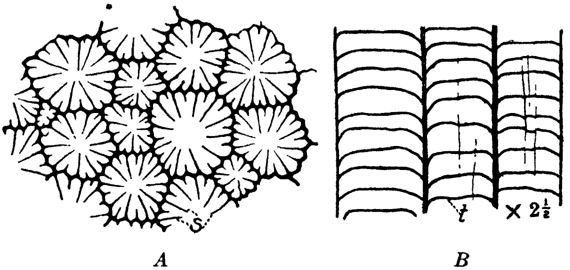


FIG. 70. — *Columnaria alveolata* Goldfuss, an abundant coral in the Ordovician seas which covered much of the present area of the North American continent. *A*, transverse section (×2½) through eleven entire individuals; *B*, longitudinal section of three of the individuals. *s*, septa; *t*, tabulæ. (From Lambe.)

It is much like Favosites, but without mural pores and with septa well developed or present as vertical ridges.

1. Sketch a group of three or four corallites, showing both sides and top; grind one corallite down until it shows the tabulæ. Label corallites, septa, tabulæ.
2. Did a single or several polyps secrete the corallites sketched? Reasons.
3. How did the polyp form the septa? the tabulæ?
4. Outline a polyp upon your above sketch.

SUPERORDER B. HEXACORALLA

Simple or composite corals with septa in cycles of six or multiples of six (whence the name from Greek *hex*, six). Corallum calcareous, horny or fleshy. Here are included the reef-building and deep-sea corals of to-day. The Hexacoralla are abundant from the Triassic to the present. The few Paleozoic (Silurian-Permian) forms referred to the Hexacoralla may belong to the Tetracoralla.

The living sea anemones belong here likewise. These possess no hard skeleton, either in the adult state or at any time during their development. They are not known in the fossil state. The brown sea anemone (*Metridium marginatum*) extends from New Jersey to Labrador; a large specimen measures 3 inches wide by 4 inches high. The orange-streaked anemone (*Sagartia luciæ*), especially abundant from New Jersey to Massachusetts, is marked by twelve longitudinal orange streaks. It is about one-quarter of an inch wide by three-eighths of an inch high.

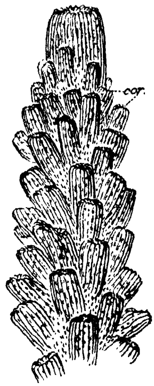


FIG. 71. — The terminal portion of a branch of a madrepore coral. The individual polyp at the tip was the largest. *cor.*, corallites, each occupied during the life of the colony by a separate individual polyp. (× 1½.)

Acropora (Fig. 71). *Tertiary to present.*

Coral compound, branching, with small, tube-shaped corallites embedded in abundant vesicular cœnenchyme. Each corallite has from six to twelve septa, which are sometimes imperfectly developed. The corallites terminating each branch are the largest. This belongs to the Madrepore family of corals. It is common off the Florida coast. (Named from Latin *acer* (*acro*), sharp, + *porus*, pore. The porous colony has spike-like corallites.)

1. Sketch five or six corallites at the tip of a branch, enlarging two times. Label corallites, septa, cœnenchyme.
2. How was the cœnenchyme produced?
3. Account for the branching of Acropora.
4. Outline a single polyp in place upon the above sketch.
5. How does Acropora aid in the formation of coral reefs?

SUBCLASS 2. ALCYONARIA

Tentacles hollow, pinnate, always eight in number as are likewise the mesenteries.

A calcareous skeleton is apparently present in all; it is usually composed of separate spicules which develop in the ectoderm

but often pass into the mesoglœa. These forms may have in addition a horny skeleton. They occur from the Ordovician to the present.

SUPERORDER A. OCTOCORALLA

Usually composite corals; skeleton calcareous, or horny, or apparently absent (name from Greek *octo*, eight, in allusion to the eight tentacles). Ordovician to present.

Tubipora. *Living.*

This red coral is composed of parallel tubes — the corallites (whence the name from Latin *tubus*, a tube, + *porus*, a pore). During the life of the colony each corallite lodges a polyp. The polyps are connected with one another by horizontal platforms which branch out from the level of the tabulæ and from which new polyps arise by budding. The skeleton is formed by the union of the spicules scattered throughout the mesoglœa.

1. Sketch (*a*) top view, (*b*) side view. Label corallites, platform, solenia tubes.
2. How do new corallites arise in the colony?
3. What are the solenia?

Gorgonia. *Living.*

Compound coral, tree-like, but branching in one plane, and all branches united to their tips by cross branches. The upbending of the ectoderm of the base forms a branched horny axis extending throughout the colony. The calcareous spicules present in the mesoglœa form a coating upon this axis in the dried specimen (whence the name from Latin *Gorgonia*, Gorgon-like, in allusion to its hardening in the air, just as the Gorgon, or Medusa, turned all beholders to stone). During the life of the colony a polyp occupied the position of each minute prominence.

1. Sketch (*a*) entire colony in outline, (*b*) a small portion enlarged four times. Note the position occupied during life by an individual polyp.
2. How was the horny axis produced? the calcareous coating?
3. What in general is the food of Gorgonia?

Superorder B. Tabulata

Composite corals; walls of corallites, thick, separate. Septa poorly developed or absent. No dissepiments present. Tabulæ numerous (whence the name from Latin *tabulatus*, furnished with *tabulæ*, tables). These occur mostly in the Paleozoic, a few only in the Mesozoic.

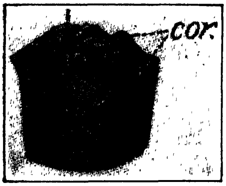


Fig. 72. — *Aulopora repens* Knorr and Walch. Natural size. A branching coral growing upon a brachiopod shell, from the Jennings formation (Upper Devonian) of Maryland. *cor.*, corallites. (From Clarke and Swartz.)

Aulopora (Fig. 72). *Ordovician to Mississippian.*

Coral very loosely compound; all corallites tube-like (whence the name from Greek *aulos*, pipe, + *poros*, a pore). Corallites attached to a foreign object by nearly their whole length. Colony produced by submarginal budding.

1. Sketch a colony, noting corallites.
2. Outline a polyp in place upon sketch.
3. How did the colony increase in size?

Favosites (Fig. 73). *Ordovician to Mississippian.*

Coral closely compound, with the corallites in contact but with separate walls. Corallites prism-shaped (whence the common name "honey-comb coral" from Latin *favus*, honeycomb). Walls perforated by equidistant pores believed to represent attempts at budding. Septa usually wanting; tabulæ numerous and conspicuous.

1. Sketch a group of five or six corallites, (*a*) top view, (*b*) side view of two. Label corallites, tabulæ, mural pores.
2. How did the colony increase in size?
3. What may the mural pores indicate?
4. How were the tabulæ formed?
5. What is the significance of the name?
6. Was the living animal able to move?

Halysites (Fig. 74). *Ordovician and Silurian.*

Coral compound, composed of long, laterally compressed corallites, and covered by a peritheca. Septa absent or repre-

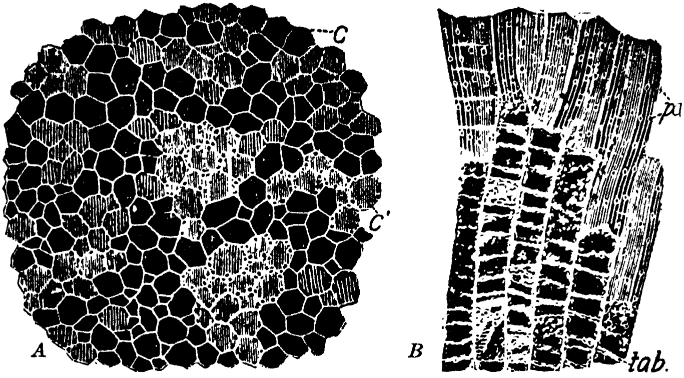


FIG. 73. — The compound "Honey-comb coral," *Favosties favosus* Goldfuss, abundant during the Niagara time. *A*, top view of colony; *B*, side view of a colony; upper portion, showing the exterior with the pores and the vertical striations; the lower portion is a section showing the granular tabulæ. *c*, corallite; *c'*, corallite with a convex tabula at the surface, margined by the characteristic pits; *po.*, pores; *tab.*, tabulæ. Natural size. (From Hall.)

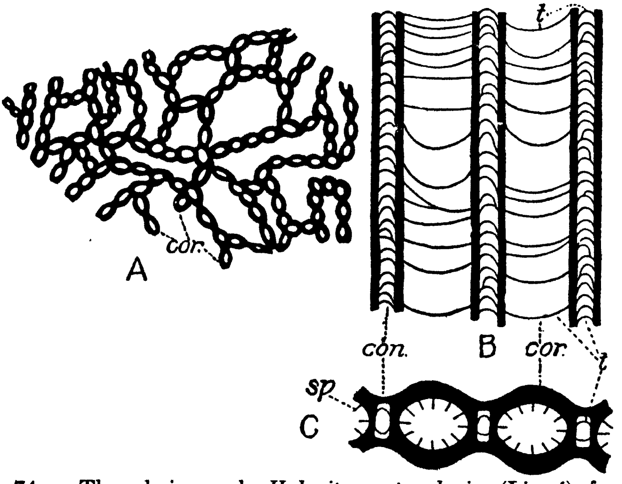


FIG. 74. — The chain-coral, *Halysites catenularia* (Linné) from the Niagara (Middle Silurian) of New Jersey. *A*, top view of a portion of a colony, natural size; *B*, longitudinal section (× 5) showing two individuals (*cor.*) with their slightly concave tabulæ (*t*), and the small connecting tubes (*con.*) with their very convex tabulæ. *C*, transverse section through the same showing the septa-like spines (*sp.*) and within the small connecting tubes a section of the highly arched tabulæ (*t*). (After Weller.)

sented by spines; tabulæ numerous. Between each pair of corallites is a small tube. Budding occurs only from one side, and the young corallites remain in contact with the parent by a constricted edge, thus forming chains, in which each corallite is a link (whence the common name, "chain-coral," from Greek *halysis*, chain).

1. Sketch an inch square portion of colony, (*a*) top view, (*b*) side view. For side view polish corallites to show tabulæ. Label corallites, tabulæ.
2. How did the colony increase in size?
3. Account for the chain formation.
4. What is the significance of the name?
5. Did each individual animal possess a separate digestive system or did it share a common one with others?

Evolution of the Cœlenterates

That these may have arisen from a protozoan group somewhat like the Dinoflagellate order of the Mastigophora, seems to be indicated by the general similarity of cell structure and the presence in both of nematocysts. An intermediate stage would necessarily be a protozoan colony in which there was a tendency among different cells to specialize in different functions, giving rise to a form like the free-swimming larval stage (the planula) of the present-day hydrozoöns. This planula is an elongated, ciliated body, with ectoderm cells without and endoderm within. In development the endoderm cells give rise to the future digestive cavity. At this stage the larva settles and becomes attached by one end, while the opposite end opens, becoming the mouth; this is surrounded by outgrowths forming the circle of food-procuring tentacles. The ectoderm cells specialized in the function of protection, the endoderm in digestion and assimilation of food. In this phylum, a tremendous forward step was taken in the efficiency of digestion, for the food is digested outside the individual cells instead of within them, as in the sponges and protozoöns. Thus here (and in all higher phyla) only liquefied food enters the individual cells. Such

efficiency in the acquirement of energy is an important step in evolution.

The radiate structure of the cœlenterate polyp may be explained as due to attachment which would necessitate a radiate method of feeding. That this radial symmetry was superimposed upon a primitive bilateral symmetry is indicated by such structures as the marked cardinal septum in the Paleozoic Tetracoralla or the fossula in its absence.

The primitive cœlenterate stock early divided into the freely floating Scyphozoa and those forms which are usually attached during one phase of their existence. Among the latter, some developed mesenteries, dividing the barrel-shaped body into vertical compartments (the Anthozoa), while the rest retained the more primitive body (the Hydrozoa and the Graptozoa).

Cœlenterata as Rock-Builders

It is only members of the classes Hydrozoa and Anthozoa that are important in this respect. Among the former it is only the hydrocorallines and the stromatoporoids which contribute at all largely to the formation of rock masses. The stromatoporoids were especially important during the Silurian and Devonian in North America and Europe, and Millepora is an important reef-builder to-day. Stromatoporoids are a very important element in the Devonian coral reefs at Alpena and Petoskey in Michigan.

The Anthozoa have been important reef-builders from the Cambrian to the present. In the Cambrian the family Archeocyathidæ, which resemble simple corals, were widespread throughout the world, even in the Antarctic region. In Labrador, opposite the Straits of Belle Isle, they form limestone beds up to 50 feet in thickness. During the Ordovician, Columnaria formed reef-like masses in North America, from Baffin Land and Alaska to the Mississippi Valley. In the Silurian, Halysites, Favosites, and Syringopora abounded. In North America the best known reefs are those of the "Great Barrier

Reef" which apparently surrounded a deep sea covering the Lower Peninsula of Michigan during the mid-Silurian (Niagaran) time. This barrier reef is made up of thousands of mound-like reefs, over a belt of fifty miles or more in width. Individual reefs are several hundred feet in diameter, with a height of 75 feet or more. The reef extends almost uninterruptedly through Ohio, Indiana, northeastern Illinois, eastern Wisconsin, the northern peninsula of Michigan, and western Ontario. The principal lime-secreting organisms in these reefs were Halysites, stromatoporoids, bryozoöns, brachiopods, and Favosites. These are recognizable, as a rule, only on the weathered surfaces, as they, with the rest of the rock, are now largely changed into a compact crystalline mass of limestone and dolomite, the change having taken place partly while still beneath the sea and partly since it has been raised into a land area (Cumings and Shrock). In Europe the coral reefs on the island of Gotland are the best known Silurian examples. These consist chiefly of such corals as Halysites and Cystiphyllum, stromatoporoids, Bryozoa, and calcareous algæ; between these the remains of brachiopods and crinoids abound.

During the Middle Devonian, coral reefs were abundant in North America, in New York, Michigan, and Iowa, in Europe in the Eifel and Belgium. The corals are chiefly the Cyathophyllidæ. Stromatoporoids are also very abundant.

In general aspect the Paleozoic coral reefs are lens- or dome-shaped masses of calcareous material with very little if any stratification, and composed of such colonial forms as corals, hydrocorallines, sponges, Bryozoa, and calcareous algæ, which grew practically where they are found. With these occur the remains of innumerable crinoids, brachiopods, mollusks, and Crustacea. In the interstices between these are sand and mud fragments of these forms, due mostly to the beat of the waves, but doubtless in some degree to the action of worms and mollusks.

In the Mississippian and Pennsylvanian, mound-like coral reefs are rare, but bedded reefs are common. In these, corals

such as Lithostrotion, Bryozoa, and brachiopods form the main mass of strata for long distances. Bedded reefs are abundant in western Alberta.

During the Mesozoic and early Cenozoic there was apparently a great reduction in the number of coral reefs, but they increased greatly from the Pliocene to the present. To-day they abound between the latitudes of 28° North and South in all oceans. A comparison of corals with other lime-secreting groups of organisms in the Funafuti coral reef is given on page 61.

1. Divide the phylum into classes and all minor subdivisions, giving an example of each.
2. In what respects are the cœlenterates an advance upon the sponges?
3. Define the four classes into which the Cœlenterata are divided.
4. Since the large jelly-fish, the Scyphozoa, consist of about 99 per cent water, how have fossil records of them been made?
5. Distinguish Hydrozoa from Anthozoa, in (*a*) the soft body, (*b*) the hard skeleton.
6. Distinguish Graptozoa from Hydrozoa.
7. Outline the probable origin of the cœlenterates.
8. How does study of the stages of growth of modern corals help in determining their probable ancestry?
9. What explanation of radial symmetry is suggested?
10. Where are coral reefs found to-day? Where did they occur in past ages?
11. What testimony do coral reefs supply as to oceanic and climatic conditions?

PHYLUM IV. CTENOPHORA (COMB-JELLIES)

Pelagic individuals with no sessile or colonial stage. Tentacles when present are usually two in number. Movement is by the large cilia which are fused into comb-like structures; these are arranged in 8 meridian-like rows or swimming plates. Not known in the fossil state. Example: Cestus (Venus' girdle).

Derivation of name. — Ctenophora > Greek *kteis*, a comb, + *phoros*, bearing, from the fusion of the large cilia to form comb-like swimming structures.

EVOLUTION OF THE CTENOPHORA

Apparently some rather primitive cœlenterates tending to develop a greater freedom of movement than the jelly-fish, evolved into the Ctenophora. Since they move through the water with the oral end forward, a biradial symmetry develops, a step in the direction of the bilateral symmetry of the higher, freely moving animals. They also developed a third layer of body cells, the mesoderm, between the ectoderm and endoderm. The mesoderm is present in all higher animals and represents a distinct advance upon the cœlenterates.

How do Ctenophora represent an advance upon Cœlenterata?

CHAPTER IX

The old phylum Vermes (Latin *vermis*, a worm) was a comprehensive group of no exact classificatory value, including soft, invertebrate animals, many bearing a general appearance to the common earthworm. This included even parasitic arachnids, crustaceans, etc., which only the study of the life history of each has placed in its proper class. The remaining members of this former group are usually divided into four phyla — Platyhelminthes (flat-worms), Nemathelminthes (round-worms), Trochelminthes (wheel-worms), and Annelida (Annulata) (ring-worms). The relationships and classification of the first three of these groups are still uncertain.

PHYLUM V. PLATYHELMINTHES (FLAT-WORMS)

Body unsegmented, usually flattened from above downward. Digestive canal is usually without an anus, the waste being carried off by the excretory system. No blood vascular system is present (except in the nemertines); the food is transported directly to the tissues through the much-branched digestive tract, which serves, as in the Cœlenterata and Ctenophora, as a gastrovascular cavity. The sexes are united in the same individual. Many forms are parasitic. This is the lowest phylum to assume a pronounced bilateral symmetry. The Nemertinea differ from the other classes of this phylum as described above in the possession of an anus, a blood vascular system, and a protrusible œsophagus. The nemertines are covered by a very slimy secretion. Fossil flat-worms are extremely rare; they are known from the Pennsylvanian to the present day.

Derivation of name. — Greek *platys*, flat, + *helmins*, worm, referring to the flattened appearance of the body.

Living examples are the Planaria (fresh water flat-worm), *Distomum hepaticum* (liver-fluke, parasitic in sheep), and *Tænia solium* (common tape-worm, parasitic in man and the pig).

PHYLUM VI. NEMATHELMINTHES (THREAD-WORMS)

Body unsegmented, long and cylindrical, with mouth and anus at opposite ends. Sexes usually separate. Mostly parasitic. Fossils extremely rare. A few examples of this and the preceding phylum have been found fossil as parasites upon insects from the upper Paleozoic coal measures and the Tertiary amber. A fossil looking much like the living round-worm Sagitta has been found in the Middle Cambrian shales of British Columbia.

Derivation of name. — Greek *nema*, thread, + *helmins*, a worm, referring to the round thread-like body.

Living examples are *Ascaris lumbricoides* (the round-worm from the small intestine of man), *Oxyuris vermicularis* (the pin-worm infesting the rectum of man), *Trichina spiralis* (parasitic in man and the pig), and Gordius (the hair-worm; parasitic in asexual generation, free in sexual; in the latter it is often 15 cm. long by 5 mm. in diameter and popularly is supposed to be derived from horsehairs which have fallen into the water).

PHYLUM VII. TROCHELMINTHES (WHEEL-WORMS)

All Trochelminthes, except the few belonging to the slightly related orders Gastrotricha and Dinophilea, belong to the wheel-worms (order Rotifera). These are microscopic in size, being the smallest of all animals except the Protozoa. The anterior end is surrounded by many variously arranged cilia, often in a circle, by means of which the animal moves. Body unsegmented. The œsophagus has a chitinous masticating apparatus. Anus present. Sexes separate. Few species are parasitic. Unknown in the fossil state.

Derivation of name. — Greek *trochos*, wheel, + *helmins*, worm, referring to the successive movements of the cilia at the anterior end of the body which gives an appearance of rotation.

Living examples are Branchionus (abundant in ponds and ditches) and Rotifer.

PHYLUM VIII. ANNELIDA (RING-WORMS)

All, except the class Gephyrea, have a ciliate, elongate body, with mouth at one end and anus at the opposite; the bilaterally symmetrical body is divided by ring-like constrictions into a series of segments representing a like segmentation within, where each segment contains a portion of the digestive canal, a pair of nephridia, a pair of nerve ganglia from the ventral chain, and blood vessels. The nervous system consists of a dorsal brain connected around the mouth with the anterior end of the double ventral nerve cord. Paired excretory organs (nephridia) conduct the nitrogenous waste matter from the general body cavity (cœlome) to the exterior.

Derivation of name. — French *anneller*, to arrange in rings, referring to the ring-like constrictions of the body.

The annelids are divided into the four following classes:

A. **Archi-annelida** *Living.*
A primitive class of Annelida. Unknown in the fossil state.

B. **Hirudines** *Living.*
Including the genus Hirudo, the leech. Unknown fossil.

C. **Gephyrea**
With larva similar to that of the Chætopoda. (Fig. 15).
Cambrian to present.

D. **Chætopoda** *Cambrian to present.*

CLASS D. CHÆTOPODA

Type of the class, *Nereis virens* (Fig. 75).

This sandworm lives in sandy or muddy beaches, usually between tide levels, under rocks or among seaweeds; at times it reaches a length of over eighteen inches. It inhabits a burrow which it makes firm by cementing the sand particles of the wall together with a mucilaginous secretion. This common form ranges from Long Island to Labrador, to Great Britain and Norway.

Its **body**, rounded above and flattened below, is divided by ring-like constrictions into a series of segments. Each segment, except the most anterior (head segment) and most posterior (tail segment), bears externally at the sides of the body a pair of outgrowths, — the flapper-like gill-feet or parapodia, which aid in creeping or act as oars in swimming. The parapodia are strengthened by chitinous rods extending outwards from the body and are bordered by several bundles of chitinous bristles. The head segment consists of two distinct portions — the

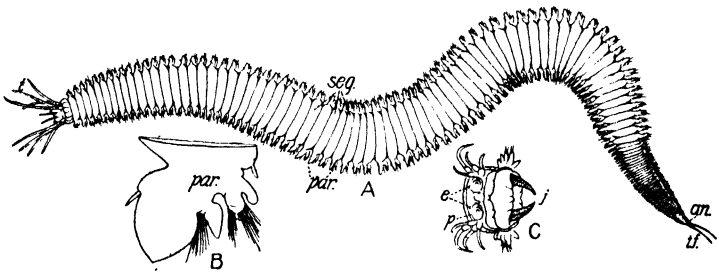


FIG. 75. — The common carnivorous worm, *Nereis virens* from Massachusetts Bay. *A*, entire worm. *B*, a paddle (or parapodium, — much enlarged) from the fifty-fifth segment. *C*, the head of another specimen, showing the toothed jaws extended. *an.*, anus; *e*, eyes; *j*, jaws; *p*, palp; *par.*, parapodium; *seg.*, segments or divisions of body; *t*, tentacles; *tf.*, terminal feelers. (A and C × $\frac{3}{8}$.)

anterior of which bears dorsally four simple eyes and anteriorly a pair of slender tentacles or feelers and a pair of thick palps; the posterior portion bears antero-laterally four pairs of tentacles. The tail segment possesses merely a pair of long terminal feelers. The body is inclosed in a very thin layer of chitin secreted by the epidermis beneath it.

Beneath the epidermis are circular **muscles** by which the worm can diminish its diameter, while beneath these are four longitudinal muscles which can diminish its length; the latter are arranged in two pairs, a dorso-lateral and a ventro-lateral pair. Besides these there are muscles to move the parapodia.

The **food** of Nereis consists of both plants and animals, but especially the latter. It is active and voracious, preying upon crustaceans and other worms, and is itself eaten by fish. By day it rests in its burrow, but at night it extends its body in search of food or may leave its burrow entirely, swimming actively about. It probably does not return to the old burrow since it easily makes a new one. The mouth is situated at the end of the head upon the under side; through this Nereis can thrust out the anterior portion of its œsophagus, by a process of rolling inside out as with the finger of a glove. This thrust-out portion, the proboscis, is provided with two laterally placed, strong, notched, black chitinous teeth. After seizing its prey with these teeth, the proboscis is rolled in again and the teeth then tear the food into pieces. The food next passes through the narrow œsophagus, into the long, straight intestine; the anus is at the posterior end of the tail segment. The intestine is regularly narrowed, corresponding to the surface constrictions. Into the œsophagus, from the glands at its sides, is poured a fluid, probably digestive in function. From within outward the walls of the intestine consist of (1) a layer of epithelial cells, (2) a layer of circular muscles, (3) a layer of longitudinal muscles, and (4) a surface membrane. The muscles promote the forward movement of the food, while the innermost layer probably aids in absorbing the digested portions of the food. Since both the anterior portion of the digestive canal to the beginning of the œsophagus, and the posterior portion within the tail segment are developmentally invaginations of the external surface, they are similarly lined with chitin.

The **blood,** of a bright red color, is carried in two main blood vessels, a dorsal tube carrying it forward and a ventral tube moving it backward; connecting these two are loops in each segment and from these loops branches are given off to the digestive canal and to the parapodia. There is no distinct heart, but in the walls of most of the blood vessels are rings of muscles which, contracting in succession, move the blood forward; the walls themselves are likewise contractile. These wave-like

contractions move the blood from behind forward in the dorsal vessel and from before backward in the ventral vessel.

Respiration takes place through the entire body surface but especially through the leaf-shaped gill-lobe attached to the upper side of each parapodium; these lobes are green at the head end of the body but bright red at the middle and posterior parts.

While the **excretion** of CO_2, etc., takes place largely through the gill-lobes of the parapodia, the nitrogenous waste (uric acid, etc.) is carried off by a pair of curved tubes (*nephridia*) in each segment.

The **nervous system** consists of a bilobed dorsal ganglion, or *brain*, situated in the anterior part of the head, connected around the mouth with the anterior end of the *ventral nerve cord* which extends to the posterior end of the body. This cord is in reality double, each part with a separate swelling or ganglion in each segment, but the two united into one by a common covering.

The **sense organs** include the tentacles and cirri as probable organs of touch, the palps used in testing food, and the four simple eyes. Each eye consists of (1) the outer cuticle, the continuation of the body chitin, (2) the cornea, the flattened cells of the epidermis, (3) the large gelatinous lens, (4) the retina, composed of many radially arranged cells, one end of each of which is continuous with the optic nerve and the other projects towards the lens as a clear, glass-like rod. The body of each retinal cell is densely pigmented for the absorption of excess light rays. Because the lens condenses the rays of light, the eye gives a much more definite perception of the direction of light than does the eye of the starfish.

The **sexes** are separate. At certain times during the summer the animals swim near the surface and cast the ova and spermatozoa into the water, where union between them later occurs. The fertilized egg develops into the adult through a series of radically different forms, one of which, the trochosphere stage, it possesses in common with mollusks as well as with other worms.

Preservable as fossils are the chitinous jaws, trails, excrement, and burrows.

1. Examine Nereis, noting the black teeth at the end of the protrusible pharynx, the eyes, body segments, parapodia, bristles.
2. What is the habitat of the animal?
3. Its food and how procured?
4. How is the food digested and the waste moved through the digestive canal?
5. How is the digested food absorbed and carried throughout the body?
6. Describe briefly (*a*) respiration; (*b*) excretion; (*c*) the nervous system; (*d*) sense organs.
7. What are the principal muscles and their uses?
8. What fossil record can Nereis leave of itself?

Summary of Chætopoda

Annelids with few or many bristles attached to the sides of the body (whence the name from Greek *chaite*, bristle, + *pous* (*pod*), foot. The class is subdivided as follows:

Order 1. Polychæta (with many setæ projecting from body wall).

(*a*) **Errantia** (Latin *errans*, wandering).

Free-swimming. Parapodia well developed. Carnivorous forms, with protrusible pharynx usually armed with chitinous teeth; these teeth are the only part of the animal found fossil. Examples, Nereis, Scolithus, conodonts.

(*b*) **Tubicola** (Latin *tubus*, tube, + *colere*, to inhabit).

Forms inhabiting a tube secreted by each individual and occupied throughout life. This tube forms the only fossil remains of the animal. Parapodia short, never used for swimming. Without protrusible pharynx and teeth. Examples, Spirorbis, Serpula.

Order 2. Oligochæta (with few setæ on body wall).

Example, earth worm.

The Chætopoda are known from the Cambrian to the present. Very many cone-shaped teeth, found in the Paleozoic from

the Cambrian to the Pennsylvanian inclusive, have received the general name of *conodonts*. Some of them may be fish teeth. These are minute, black, and lustrous, extremely variable in form. Chemically, some appear to be composed of chitin, others of phosphatic carbonate of lime.

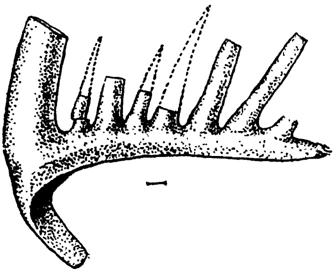


FIG. 76. — A conodont (an imperfect jaw probably of an annelid worm) Prioniodus, from the Genesee (Devonian) of New York. The projections were pointed; three of these have been restored. Enlarged; true size indicated by line below.

Prioniodus (Fig. 76).

Ordovician to Devonian.

A conodont of this form consists of a narrow basal part which supports many, usually five to twenty, small teeth, besides a long tooth situated anywhere from the middle to the end of the basal portion. This long tooth is always continued below the basal part. These conodonts probably corresponded in position and function to the teeth of Nereis, or those of primitive fish. The name, from Greek *prion*, a saw, + *odous*, a tooth, refers to the saw-like arrangement of the teeth.

1. Sketch a specimen, enlarging it three times.
2. What is the significance of the name?
3. What general name is applied to all such teeth?
4. In what part of the living animal were these? Their function?

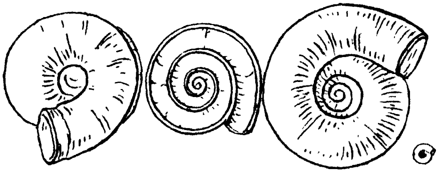


FIG. 77. — A tube-building worm, *Spirorbis borealis* Daudin, belonging to the class Chætopoda, abundant upon seaweed, etc., off the New England coast. The small one to the right is natural size. The middle of the enlarged three is a section of the shell.

Spirorbis (Fig. 77).

Ordovician to present.

Minute, calcareous, spiral tubes (whence the name from Latin, *spira*, spire, + *orbis*, circle). These tubes are cemented by their flat underside to some foreign object.

1. Sketch a tube.
2. How could the body of the animal within cement this to some foreign object?
3. Could the animal leave its tube and later return to it?

Serpula (Fig. 78). *Silurian to present.*

These build firm, irregularly contorted calcareous tubes,

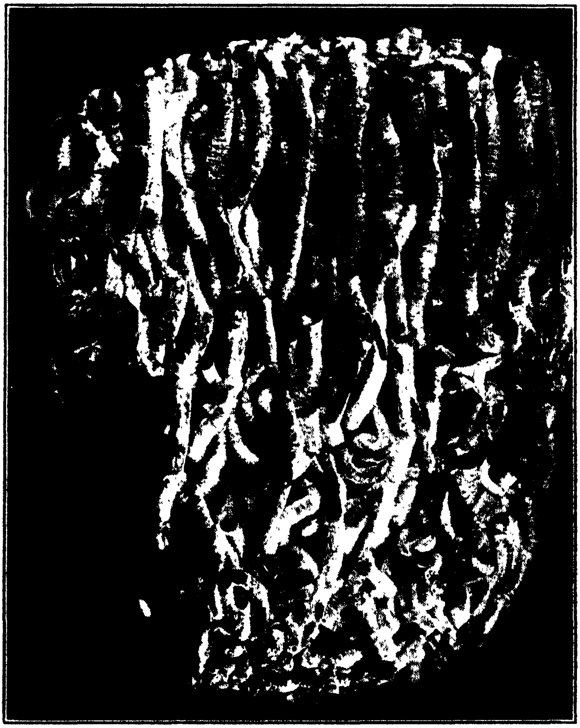


FIG. 78. — Serpula ($\times \frac{2}{3}$).

which are at times free but are usually attached to shells or to one another. The name, from the Latin *serpere*, to creep, refers to the contorted tubes.

1. Sketch a tube.
2. Why is Serpula a more important rock-builder than Spirorbis?

Scolithus (Fig. 79). *Cambrian to Silurian.*

Merely straight, filled tubes, without any organic characters preserved. Origin doubtful. They may have been formed by such an animal as the living Nereis. The mucus secreted by the body surface would cement the sand grains surrounding the burrow, which would thus acquire a stability so that it could remain uncollapsed until filled by drifting sands.

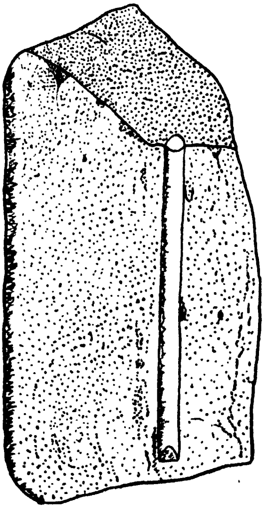


FIG. 79. — *Scolithus linearis* Hall. Upper Cambrian of eastern North America. Natural size.

1. Sketch a Scolithus.
2. How could this have been formed?

EVOLUTION OF THE "WORMS"

The four phyla of " worms " represent offshoots from some primitive cœlenterates in which an innate urge to move forward counteracted the downpull of gravity to a sessile life. A forward motion continued for many generations in a primitive group tends to develop a main nerve ganglion or brain in the anterior end of the body, since it is the part of the body which is directed forward that first comes into contact with food and danger. The sensations resulting from these encountered stimuli develop nerve cells in the region of greatest excitation. Since the right and left halves of the body move equally and are equally stimulated, they tend to develop similar characteristics. Thus representatives of each of these very dissimilar phyla have an anterior brain, a bilaterally symmetrical body and, with the exception of the Trochelminthes, a circumœsophageal nerve ring. In all animals, the getting of energy through eating is the most important activity of life and calls for an early development of nerves around the œsophagus. Such

a nerve ring is present in practically all classes of invertebrates above the cœlenterates and Ctenophora. In the vertebrates this function is performed by the greater ramification of nerves from the brain and spinal cord.

The many and varied structural forms included under the old term "worms" have made their classification extremely difficult. It is seen, however, that the animals radiated in many directions, both in habitat and in the getting of food. Very many deserted the free life of their ancestors for the life of the parasite, a life calling for less expenditure of energy.

"Worms" as Rock-Builders

The only worms capable of adding to the growth of strata are various chætopods of the Annelida phylum. Teeth of the carnivorous forms are at times abundant, especially the problematical conodonts, though they never form more than a small percentage of the rock. The tube-builders, however, are more important, especially the serpulids from the Jurassic to the present, for by the time of the mid-Mesozoic they had become sufficiently gregarious to form masses of tubes of considerable thickness. In northern Germany, the Jurassic Serpulit beds attain a maximum thickness of 230 feet; these only at intervals include limestone beds which are composed almost entirely of fragments of Serpula.

1. Divide the phylum Annelida into classes and all minor subdivisions, giving an example of each.
2. Briefly outline the evolution of the "worms."
3. Discuss "worms" as rock-builders.

CHAPTER X

PHYLUM IX. ECHINODERMATA

Typically radially symmetrical marine animals with a skeleton of calcareous plates or spicules embedded in the skin. The arrangement of the skeletal plates and of the internal organs is usually pentamerous, the numeral five being thus the governing number of the echinoderms. They are likewise characterized by the presence of a water vascular system which functions in respiration and movement. Without a single exception all echinoderms are inhabitants of the ocean.

They represent an advance upon the Cœlenterata in the presence of a digestive tube distinct from the body cavity (cœlome), in their more highly developed nervous system, in the possession of a " blood " vascular system, and in an almost exclusively sexual mode of reproduction.

The seven classes of the Echinodermata form a more or less closely related group. If the comparison is made with considerable latitude, the arms of the starfish and crinoid are homologous to the ambulacra of the cystoid, blastoid, and echinoid; moreover, if the starfish be placed with mouth uppermost, the lower side of the central disk corresponds to the base of the cystoid, blastoid, and crinoid, while the upper side with its central mouth and radiating ambulacra is similar to the upper side of these classes, and internally the position of the ambulacral, blood vascular, and nervous systems is then similar; in echinoids, a like orientation with the starfish may be made by bending the arms of the latter until they almost meet dorsally (Fig. 80).

The three classes, cystoids, blastoids, and crinoids, are intimately related; the mouth is turned upwards and the indi-

viduals are usually fixed to some foreign object. The blastoids are nearest to the cystoids, the hydrospire probably corresponding to the pore-rhombs, while the position of mouth and anus is approximately the same in both. The hydrospires of blastoids are likewise correlated with the pores beneath the arm bases of certain crinoids, such as Batocrinus. In the three classes, starfish, brittle stars, and sea urchins, the mouth is

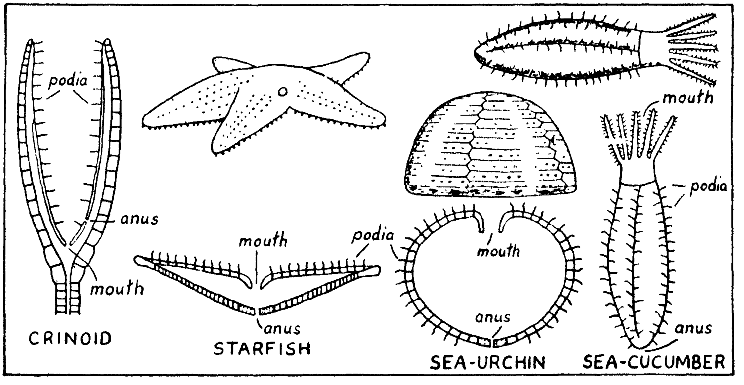


Fig. 80. — The upper row gives the living position of the principal stalked and free echinoderms. The lower row is arranged to show the similarity of structure.

turned downward, and the animals are unattached, able to move freely from place to place.

Derivation of name. — Greek *echinos*, hedge-hog, + *derma*, skin, in allusion to the spines possessed by many of the members of this phylum.

The Echinodermata are divided into the following seven classes, the first three being often grouped together under the Subphylum Pelmatozoa.

Type of the phylum Echinodermata, *Asterias forbesi,* the starfish (Fig. 81).

Asterias forbesi ranges from Maine to the Gulf of Mexico, but is very common only south of Cape Cod, living from high

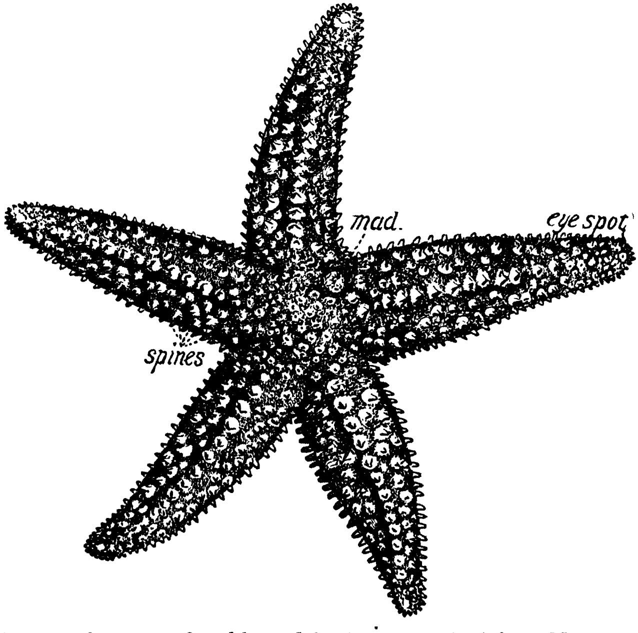


FIG. 81. — A four-months-old starfish, *Asterias forbesi,* from Narragansett Bay, Mass. Natural size. *mad.*, madreporite. (From Mead.)

tide line to a depth of one hundred feet. In summer and autumn it lives in rocky places in shallow water, but seeks greater depths in winter.

The starfish is a free-moving animal, consisting of five rays or arms united broadly to a central portion, the *disk.* The mouth

is situated in the center of the under or ventral side of this disk, and the anus correspondingly nearly in the center of the dorsal surface. From the mouth radiate five grooves, one in the middle of each arm ; these grooves are called the *ambulacral grooves,* or ambulacra.

Into each of the *ambulacral grooves* project four rows of soft tubular bodies with sucker-like extremities. These are the *tube-feet,* the locomotive organs of the animal ; they form a part of the **water vascular** system which is especially characteristic of the echinoderms. This system consists of a series of tube-like passages filled with sea water. The water is admitted through a finely perforated plate, the *madreporite,* situated on the dorsal side near the junction of two of the arms. From the madreporite an S-shaped tube, the madreporic or *stone canal,* descends to the ventral side of the animal and connects with a five-sided ring-like canal surrounding the mouth. From this ring-vessel radiate the five straight ambulacral vessels to the extremities of the five arms. Along each of these radial tubes are given off the four rows of tube-feet. Each of the tube-feet (podia) is a small muscular tube, closed at one end and expanded at the other into a bladder-like *ampulla.* The ampullæ are inside the arm, protected by the dermal plates, while the small closed end extends between the plates, protruding out into the arm furrow and ending in a disk-like expansion. Sea water is admitted from the radial ambulacral vessel of the arm into the ampulla ; by the contraction of this it is forced into the corresponding tube-foot, which thus becomes greatly lengthened. When the foot is thus extended and comes into contact with a stone or other solid object the water is withdrawn from it, the middle of its tip is drawn inward, forming under it a vacuum, and thus the disk-like end of the foot is converted into a sucker which clings to the rock. When water is again forced into the foot by the ampulla, the hold of the sucker is relaxed. Thus the many tube-feet acting independently reach forward in the general direction of **locomotion,** attach themselves to some foreign object, and through contraction pull forward the entire body

with a slow gliding motion, while the other feet already contracted loose their hold and then reach forward. A fair speed is six inches a minute. Although a starfish can move in any direction, it usually proceeds with the arm lying immediately to the left of the madreporic plate in advance.

The **skeleton** or test consists of many calcareous plates embedded in the sub-epidermis (mesoderm), which, except at the mouth, completely surrounds the body. Since the cells of the mesoderm have the power of absorbing and redepositing lime, the internal skeleton thus formed changes in shape and size as the animal grows. In origin the skeleton of echinoderms is thus more comparable with the bones of vertebrates than, for example, with the shells of mollusks. The plates of the echinoderm skeleton are crystalline and are thus easily distinguished even as very small fragments. Since bands of muscular fibers extend between all contiguous plates, the arms and disk are movable. The protective spines are covered only by the epidermis.

The chief **food** of the starfish is mollusks (especially mussels, clams, and oysters), barnacles, worms, small crustaceans, and bits of decaying matter. The smaller bits are passed by the tube-feet into the mouth. In securing larger food, such as a clam, the starfish folds its arms about its prey, attaching its hundreds of tube-feet to the valves of the shell, and through the steady pull thus exerted tires the large adductor muscles of the mollusk. Experiment has shown that a large starfish can exert a steady pull of over two and a half pounds. Between the valves thus opened the starfish rolls its very distensible stomach in the form of a thin sheet spread over the soft tissues of its prey. Then the great digestive glands in the upper part of the stomach and in the arms pour out their secretion through the tubular passage remaining in the center of the sheet, and the food is rendered fluid and absorbed. The stomach then contracts and is rolled back through the mouth into the body. The starfish may live for months practically without food, but when opportunity offers it will eat many mollusks, one immediately

after another. It opens gastropods (periwinkle or conch) in a similar manner by attaching the tube-feet to the operculum and shell.

The upper, narrow portion of the stomach has long divisions, one extending to the end of each arm. These divisions secrete a digestive fluid which converts starch into sugar, proteids into peptones, and emulsifies fat. The resulting chyle passes by osmosis into the body fluids; these are kept in motion by cilia, and thus the products of digestion are carried to all parts of the body. There is no heart or regular circulatory system.

Respiration takes place (1) through the short, hollow, thread-like processes (dermal branchiæ) which extend out through microscopic pores between the plates over the whole body and open directly into the cœlome, and (2) through the ambulacral system, the oxygen entering through the tube-feet and madreporite.

The **nervous system** has three divisions, (1) the epidermal, a pentagonal nerve ring around the mouth, from each of the five angles of which one radial nerve fiber extends below the radial ambulacral vessel to each eye-spot; (2) the deep portion, a double pentagon around the mouth, of which each angle sends a nerve to each arm; and (3) the cœlomic, the nerves extending along the top of each arm.

The **sense organs** include that of smell and the so-called eye. At the tip of each arm is a bright red speck, the eye-spot. This is practically nothing but a collection of pigment granules upon the expansion of nerve cord; since there is no lens there can be no image, and hence the animal can probably distinguish light and color, but not form. The perception of light is probably merely the sensation of warmth due to the absorption of the light rays by the pigment and their consequent conversion into heat.

Over the eye is a tentacle similar to a tube-foot, but smaller and without the sucker. Experiments have determined its function to be that of smell, and that the animal is guided to its food more by this sense than by sight.

Reproduction is exclusively sexual, with the sexes in separate individuals. The eggs and spermatozoa are discharged into the water in great abundance during the last three weeks of June, although they are also found during the summer and occasionally even during the winter. The eggs after fertilization develop into little transparent bilateral larvæ covered with waving cilia. At this time their greatest enemy is the menhaden. They swim about slowly near the surface and feed on minute organisms until they attain a length of an eighth of an inch. Then the star shape begins to develop and in a few hours a very small star lies at the bottom of the ocean. These settle on seaweeds and eel grass and begin at once to devour the young clams which have likewise begun life here. It has been found that one of these little starfishes devoured over fifty young clams somewhat smaller than itself in six days. Their growth depends upon the amount of food eaten, and hence the age at which a female begins to produce eggs is said to vary from one to six years. A starfish can regenerate lost arms.

1. Sketch (*a*) ventral view, (*b*) dorsal view. Label disk, arms, ambulacra, tube-feet openings, mouth, eye-spots, madreporite, anal plate, spines.
2. Give the habitat of Asterias.
3. How does it move?
4. What is its food? Describe how it eats.
5. How is the food digested? assimilated? waste expelled?
6. What protection against enemies has Asterias?
7. Is the skeleton (test) external or internal? Explain.
8. How does the animal respire?
9. Of what does the nervous system consist? Its use?
10. Describe the sense organs.
11. Outline briefly its development from the egg to the adult.
12. How long does it take to mature?
13. What makes the starfish such an enemy to oyster and clam culture?
14. Can a starfish regenerate lost parts? Why is this advantageous to the animal?
15. In what respects are the echinoderms more highly evolved than the cœlenterates?

CLASS A. CYSTOIDEA (SEA-CYSTS)

Calyx usually stemmed. Mouth nearly or quite central upon the upper (ventral) surface. From the mouth radiate usually two to five or more simple or branching ambulacra; along these in life food particles could pass to the mouth, probably driven by numerous cilia. These food grooves may be upon the outer surface of the calyx plates, between them, or upon their inner surface, and are rarely extended into free branches, the arms. Anal opening excentric, often closed by a valvular pyramid.

Calyx plates usually irregularly arranged, varying in number from thirteen to several hundred; as a rule a few, or all of the plates, are pierced by pores which are either irregular or arranged in rhombic figures, with half of the rhomb on one plate and half on an adjoining one; the pores from opposite plates are united by closed straight ducts which may have functioned in respiration.

Cystoids are the oldest and least specialized group of the Pelmatozoa (which include cystoids, blastoids, and crinoids), and probably represent most nearly the ancestral type of the three classes.

They are extinct, being confined entirely to the Paleozoic. They extend from the Cambrian to the Mississippian, inclusive, with maximum development in the Ordovician and Silurian.

Derivation of name. — Greek, *cystis*, bladder, + *eidos* (*oid*), form, in allusion to the globular shape of most of the species.

Caryocrinus (Fig. 82). *Ordovician and Silurian.*

The principal portion of the body, a sub-globular hollow ball, called the *calyx*, contained the digestive and blood vascular systems. This calyx was anchored to the ground by a long, jointed stem. The food grooves (ambulacra) radiating from the mouth terminate in six to thirteen feeble arms. Both mouth and food grooves are within the upper part of the calyx. Upon the outer surface of each calyx plate, except that at the summit, are five or six single or double rows of pores radiating from its center. Each of these pores is prolonged upon the inner sur-

face of the plate into a straight calcareous tube which in turn opens by a pore upon a bordering plate. All the tubes thus uniting across the straight suture of two contiguous plates form in outline a rhomb. The function of these *pore-rhombs* is supposed to have been respiratory.

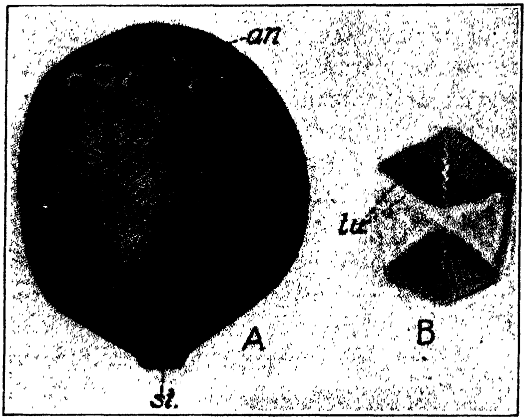


FIG. 82. — *Caryocrinus ornatus* Say, from the Niagara shales (Middle Silurian) of western New York. *A*, calyx of a large specimen (natural size) with stem and arms missing. *B*, inside of one of the plates (slightly enlarged), showing the water tubes, with openings at their inner ends. *an.*, anus, protected by a valvular pyramid; *st.*, position of stem; *tu.*, tubes. (After Hall.)

Caryocrinus is thus somewhat similar to a starfish turned mouth side uppermost, with an anchoring stalk attached to the dorsal side, the mouth and much of the ambulacra concealed by calcareous plates, and with the ends of the ambulacra branching into free arms. Since the mouth was concealed, it was necessary that food be passed into it through the ambulacral grooves by the cilia lining them.

1. Sketch (*a*) side view, (*b*) a plate enlarged twice. Label calyx, place of attachment of stem and of arms, plates forming the ventral surface of calyx, pores.
2. What was probably the function of the pores?

3. Of what did the animal's food probably consist? How did it procure it?
4. Compare Caryocrinus with a starfish.
5. What was its habitat? Reasons.
6. What part of the living animal does the fossil represent?
7. What animals living off our coast are likewise fastened to the sea-bottom?
8. What characters show the cystoids to be primitive unspecialized types?
9. Give the geologic range of the cystoids.

Agelacrinites (Agelacrinus) (Fig. 83).

Ordovician, rare in Silurian and Devonian.

The animal is circular, flat, stemless, cemented temporarily or permanently, by the entire lower (dorsal) surface to a foreign object, usually a brachiopod shell. The hard protecting calyx is composed of many thin, flexible, and more or less overlapping plates; these are perforated by pores, which probably had a respiratory function. From the centrally placed mouth, which is covered by four plates, radiate five curved, unbranched, covered food grooves. The anus is situated between two of the food grooves and is roofed over by a low pyramid of plates (Name from the Greek *agele*, a group or herd; several individuals were grouped together on the slab from which Vanuxem in 1842 described the genus.)

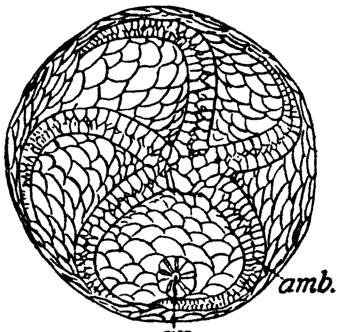


FIG. 83. — A cystoid, *Agelacrinites cincinnatiensis* Rœmer, from the Ordovician of Cincinnati, Ohio. Top view (× 2) showing the curved ambulacra (*amb.*) within which are the covered food grooves. Anus (*an.*) nearly marginal. (Redrawn from Meek.)

This genus and the many other forms similar to it are often placed together in a distinct class, the *Edrioasteroidea*, extending from the Cambrian to the Mississippian. These are characterized by a circular test composed of an indefinite number of

irregular plates, permanently attached or adhering limpet-like with some power of movement; mouth above.

1. Sketch surface view, noting calyx, mouth, anus, ambulacra.
2. How, probably, did the animal procure its food?

CLASS B. BLASTOIDEA (SEA-BUDS)

Calyx ovate, short-stemmed or stemless; distinct arms absent, existing only as pinnules. Around the central mouth are five or ten spiracles which are connected internally with the hydrospires — canals probably respiratory in function. Some forms have a distinct anal opening; in others this opening is fused with one of the spiracles. From the mouth radiate five ambulacral areas.

The class is entirely extinct and confined to the Paleozoic, ranging from the Ordovician to the Permian.

Derivation of name. — Greek *blastos*, bud, + *eidos* (*oid*), form, in allusion to the bud-shaped calyx of most species.

Pentremites (Fig. 84). *Mississippian.*

This differs in general from the starfish in its bud-shaped body (*calyx*), which was anchored to the ground by a short, jointed stem attached to its dorsal surface; the mouth, or ventral side, was thus uppermost. The calyx inclosed the digestive and blood vascular systems. In the center of the upper surface is a five-angled opening, the mouth, surrounded by five round openings, the *spiracles*. From each angle of the mouth radiates a food, or ambulacral groove, and from this groove branch off smaller side grooves almost at right angles, the whole forming a V-shaped ambulacral area.

At the upper end of each side groove is a small pore (*marginal pore*); these pores open upon the inside of the calyx into a calcareous canal looking like a much-folded bag, the *hydrospire*, probably respiratory in function. Each of the five pairs of hydrospires from adjoining ambulacra ends in one of the spiracles. During life, it is probable that a current of water passed in at the marginal pores, through the hydrospires, and out at the

spiracles. Around the marginal pores were long, jointed pinnules which functioned in straining out the food particles; this food, probably similar to that of crinoids, was urged down the side grooves by the cilia lining them, and thus down the central groove to the mouth. In exceptionally well-preserved specimens the central and side food grooves to the base of the pinnules are roofed over by very minute plates.

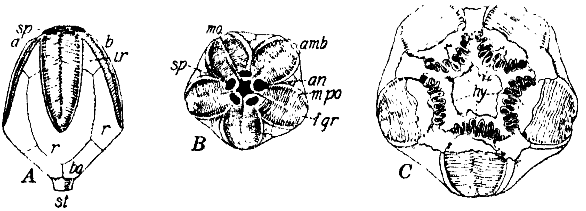


FIG. 84. — This blastoid, *Pentremites pyriformis* Say, was very prolific in the clearer portions of the sea (*i.e.*, Kentucky, Alabama, and Mississippi), which covered much of North America during Kaskaskia (Upper Mississippian) time. *A*, side view (natural size) with stem missing, as is nearly always the case. *B*, top view. *C*, cross section (× 2) at *a–b* in *A*. *amb.*, ambulacrum; *an.*, anal opening fused with a spiracle; *ba.*, basal plate; *f.gr.*, food groove; *hy.*, hydrospires (to conduct water from the marginal pores out through the spiracles); *i.r.*, interradial plates; *m.po.*, marginal pores; *mo.*, mouth; *sp.*, spiracles; *r*, radial plates; *st.*, place of attachment of stem.

The position of the pinnules is indicated by minute pits and knobs.

Little is known concerning the digestive, blood vascular, and nervous systems; there is some evidence of radial nerve cords connected with an oral ring, and of radial blood vessels likewise connected with an oral ring. The anal opening is fused with the largest spiracle.

The calyx has thirteen definitely arranged calcareous plates — three basals, five large incised radials, and five interradials or deltoids. The plates are firmly united. The structure of the stem is similar to that of the crinoids.

Pentremites was exceedingly abundant in the sea which covered most of North America during Mississippian time.

1. Sketch (*a*) side view, (*b*) ventral view. Label calyx, mouth, spiracles, ambulacra, marginal pores, anal opening, place for attachment of stalk.
2. Explain the process by which the animal ate.
3. How did it probably respire?
4. Compare it with a starfish.
5. Give the geologic range of Pentremites.
6. What was its habitat?
7. What part of the living animal does the fossil represent?
8. Could the animal move? Give reasons.

CLASS C. CRINOIDEA (SEA-LILIES)

The body (calyx), more or less globular, is fastened, temporarily or permanently, to some foreign object by means of a stalk arising from its dorsal (lower) surface. The ventral (upper) surface bears the mouth, which is usually central, the anus, which is eccentric, and the ambulacral grooves. These grooves extend into the more or less complexly branched arms, which are usually bordered with pinnules. Some forms, as Eucalyptocrinus, were attached by roots; some, as Pentacrinus and Ancyrocrinus, anchored themselves to seaweeds and other objects by processes from the lower end of the stalk, and some probably used their stems for coiling around a support.

Crinoids range from the Cambrian to the present time, though they were most abundant in the upper Paleozoic. Owing to their gregarious habits, their skeletons form the chief part of great masses of limestone (hence called crinoidal limestone), especially in the Devonian and Mississippian periods. Living crinoids are mostly found at moderate depths, though they range from deep sea to shallow water.

Fossil remains of these animals consist mainly of detached portions of stems or scattered calyx plates. Complete forms, preserving calyx, stem, and root, are rare.

Derivation of name. — Greek *crinon*, lily, + *eidos* (*oid*), form. The stalked forms resemble lilies, as is noted also in the common name of the class, " sea-lilies."

Pentacrinids (Fig. 85). *Triassic to present.*

These forms, unlike the starfish, have the mouth, or ventral side, uppermost, while the opposite, or dorsal, side is fixed to the ground by a long flexible stalk.

The animal is composed of a globular body (*calyx*), from the upper surface of which branch arms, and from the lower surface is given off the stalk. Embedded within the skin of all parts are many calcareous plates forming a strong protective skeleton. The *stalk* is made up of grooved disks, resting one upon the other like a pile of coins, and pierced at the center by a canal containing a prolongation of the nervous and blood vascular systems. Small branches, the *cirri*, whose function is doubtful, are given off from the stem and have an internal and external structure similar to that of the stem. In some cases, probably, the stalk was attached to the ground by a branching root; more generally it was free, being merely anchored to seaweeds, etc., by the entwining of the cirri at its lower end. The stalks are very long, attaining at times a length of at least twenty feet.



Fig. 85. — Above, stem joints of *Pentacrinus asteriscus* M. & H., from the Jurassic of Montana. To the left the surface view of a joint (natural size); to the right five joints, side view. Below, a modern Pentacrinid (much reduced), from the Gulf of Mexico. The last is reproduced from Lucas' "Animals before Man in North America." Copyright, 1902, by D. Appleton and Co.

The calyx is made up dorsally of calcareous plates definitely arranged; the plates upon the ventral surface are without definite order. All the plates are firmly united, forming a rigid skeleton. The mouth occupies the center of the upper surface and from it radiate five open ambulacral or food grooves to the tips of the arms. These arms, unlike the usually simple ones of the starfish, branch repeatedly, each

branch in turn giving off many short side branches or *pinnules.* The ambulacral grooves branch correspondingly. These grooves are lined with cilia by the aid of which the food, chiefly diatoms, protozoöns, and microscopic crustaceans, is urged into the mouth. The ambulacral system here, as in the starfish, forms a ring around the mouth and sends a ray to each pinnule; connected with this ring are several ciliated, branched water-tubes opening into the cœlome. Into this cœlome, the body cavity, water enters from the exterior by means of minute water-pores through plates on the ventral surface. Small, distensible tube-feet (the tentacles) are present along the outer edges of the ambulacral grooves; they, however, lack suckers, and are not locomotor but merely tactile and respiratory in function. The water-pores and water-tubes represent the madreporite and its canal of the starfish.

The mouth opens through an œsophagus into a wide stomach, thence into the intestine, which coils inside the body wall, but does not have extensions into the arms. This opens by the anus through a tube eccentrically placed upon the upper (ventral) surface.

The *nervous system* consists of (1) the ambulacral portion, a ring around the mouth from which pass series of nerves to arms and pinnules through the base of the ambulacral grooves; and (2) the axial portion, a five-angled organ beneath the basal plates at the junction of calyx and stalk, from which radiate nerves through the center of the arm and pinnule plates and to the stalk. A transverse section through an arm would thus show a water tube and a nerve cord directly beneath the food groove, while deep within the calcareous plate is lodged a second nerve cord.

The sexes are separate. The dilated pinnule bases lodge the ovaries and testes.

The stalk is five-sided throughout in ancient fossil species (*e.g.*, *P. asteriscus*) but in living forms only near the calyx. New plates are added directly beneath the calyx; these are in living pentacrinids at first five-sided like the entire stalk of lower Meso-

zoic species; but later they become round. These changes, in which the animal recapitulates its ancestry, may be noted in a single individual from the small plates directly beneath the calyx to the large ones at the lower end of the stalk. The young stem joints are more porous than older ones, and therefore not so apt to be preserved fossil.

The range of the Pentacrinidæ family is from the Triassic to the present. The symmetrically pentagonal stem joints of *Pentacrinus asteriscus* are very abundant in the Jurassic of the western part of North America. Living forms occur in many oceans. A common West Indian genus is Isocrinus.

1. Sketch a side view, noting calyx, arms, pinnules, stalk.
2. Compare it with the starfish.
3. How and what do the Pentacrinids eat? How breathe?
4. Of what does the nervous system consist?
5. Could the animal move? Give reasons.
6. Is the skeleton external or internal? Illustrate by means of a plate of the stalk.
7. Make a transverse section of a pinnule; label and sketch in sufficient soft parts to show how the food was transferred, etc.

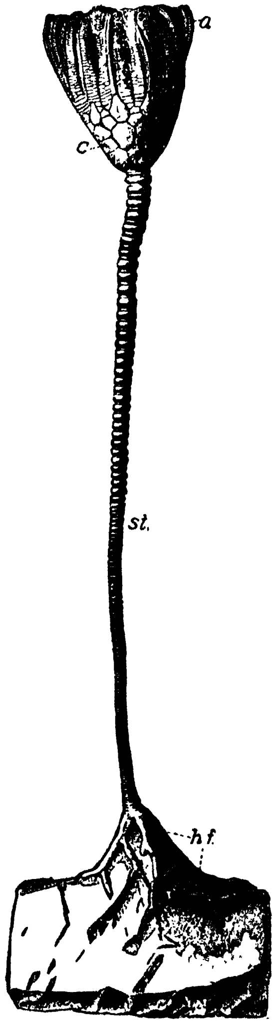


FIG. 86.—*Eucalyptocrinus crassus* Hall, from the Middle Silurian of Indiana. *a*, arms; *c*, calyx or cup; *hf.*, holdfasts, the rootlike basal part for attachment to the ground; *st.*, stalk. Slightly reduced. (From Hall.)

8. What is the significance of the name crinoid?
9. What is the evolutionary significance of the fact that the plates of the stalk immediately below the calyx are five-pointed, but later become rounded?

Eucalyptocrinus (Fig. 86). *Silurian, rarely Devonian.*

Calyx with a deep concavity at the stem end. Attached to the elongate ventral portion of the calyx and extending its full length are ten vertical partition plates; in each of the ten compartments thus formed are lodged two arms, which never extend upward beyond the calyx.

1. Sketch a side view, noting calyx, vertical partitions, arms if preserved.
2. In what conspicuous feature does this genus differ from most other crinoids?

CLASS D. ASTEROIDEA (STARFISHES)

Body free, star-shaped, with a central disk and hollow arms (usually five in number), each containing a prolongation of the organs of the body. Movement is by means of the tube-feet which project between the plates from the five ambulacral grooves radiating from the mouth. These grooves correspond to the food grooves of the crinoids.

Asteroidea range from the Cambrian to the present. Living examples include *Asterias vulgaris* and *Asterias forbesi* (p. 196), the common starfishes of the Atlantic coast, the former north and the latter south of Cape Cod. There are many tropical species.

Derivation of name. — Greek *aster*, star, + *eidos* (*oid*), form, in allusion to the star-shaped body.

Paleaster (Fig. 87). *Ordovician to Mississippian.*

Differs from Asterias in having the two rows of ambulacral plates but slightly inclined to each other, the plates from the opposite sides alternating, in the very large marginal plates and in having two, instead of four, rows of tube-feet.

1. Sketch a specimen.
2. Is it a dorsal or a ventral view?
3. How does it differ from Asterias?

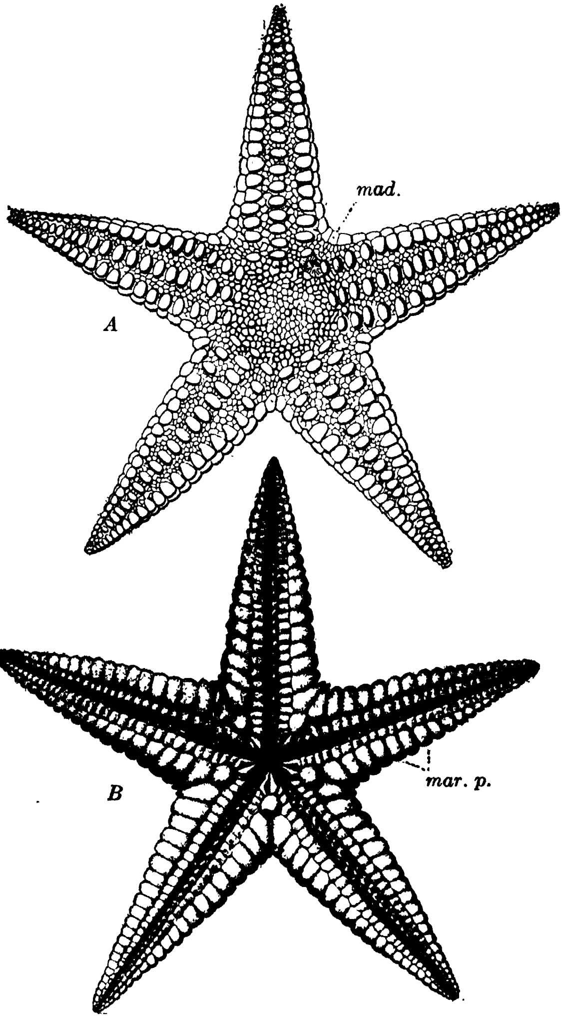


FIG. 87. — *Paleaster eucharis* Hall, from the Devonian of New York. *A*, dorsal side, showing the madreporite (*mad.*). *B*, ventral side, showing the centrally placed mouth and the large marginal plates (*mar. p.*). (After Hall.)

CLASS E. OPHIUROIDEA (BRITTLE STARS)

The ambulacral and digestive systems are confined to the central disk; otherwise in external appearance much like the Asteroidea. Movement is by wriggling by means of the slender, rounded arms; these are quite sharply marked off from the central disk. Tube-feet, protruded at the sides of the arms, lack sucking disks and have no ampullæ; they serve for touch and respiration only. No anal opening is present. Mouth and madreporite are ventral.

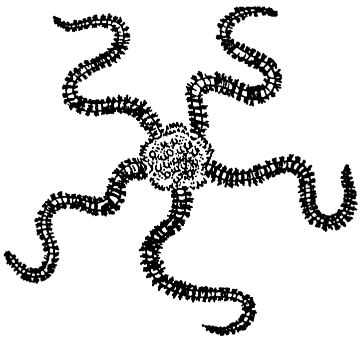


FIG. 88. — *Ophiopholis aculeata* Gray, from the coast of New England. The brittle starfish. Dorsal view (× ½). (From Verrill and Smith.)

The range of the class is from the Ordovician to the present. Living forms are more commonly inhabitants of deep than of shallow waters. *Ophiopholis aculeata* (Fig. 88), the "brittle starfish," is abundant at a depth of one to one hundred feet in rocky crevices from the coast of New Jersey to the Arctic Ocean and is likewise common on the Pacific coast and in northern Europe.

CLASS F. ECHINOIDEA (SEA URCHINS)

Free-moving animals, usually with a globular or disk-shaped body, a perambulating dome. Skeleton (*test*) rigid, formed of firmly united calcareous plates, or more or less flexible with imbricating plates, covered with movable spines. Mouth ventral and central, or anteriorly eccentric, with (except in the adult spatangoids) a complicated masticating apparatus, the Aristotle's lantern. Madreporite dorsal, in the right anterior genital plate; this plate orients the sea urchin, the antero-posterior axis passing through the ambulacrum on its left and

through the opposite interambulacrum. The anal opening is dorsal, in the posterior interambulacrum.

Straight or variously arranged ambulacral areas run from the dorsal to the ventral surface.

Movement is by means of the elongated tube-feet which pass through, not between, the plates. Many forms in addition move by means of their spines, often quite rapidly.

Sea urchins are gregarious, frequently occurring in such abundance as to pave the surface of the rock and the bottom of tide pools in sheltered places. On exposed coasts, many forms bore cavities by their teeth or by absorption into calcareous and non-calcareous rocks. Common examples are Strongylocentrotus, on the Atlantic coast north of Cape Cod; Arbacia, on the Atlantic coast south to Florida; Echinarachnius, the "sand dollar," on sand beaches from New Jersey northward and on the Pacific coast.

Echinoids are known from the Ordovician to the present.

Derivation of name. — Greek *echinos*, a hedge-hog, + *eidos* (*oid*), form, referring to the spines so characteristic of all members of this class.

Strongylocentrotus (Figs. 89, 90). *Upper Tertiary to present.*

This differs from the starfish in its globular form, which is slightly compressed dorso-ventrally. The calcareous plates are firmly fitted together like a mosaic, forming a rigid shell. The entire surface, except the region around the mouth, is thickly studded with many rounded tubercles, to which are attached solid spines which are movable by muscles on ball and socket joints (Fig. 90, *B*). Corresponding to the five ambulacral grooves of the starfish are five slightly expanding *ambulacral areas* (*ambulacra*) extending radially from near the center of the dorsal to the ventral side. Each ambulacrum consists of two narrow columns of plates through which the long, sucker-bearing tube-feet protrude (Fig. 90, *A t.f.*); the middle of the area is without pores for tube-feet and bears numerous spines. The tube-feet number about 1800, and can be protruded beyond the longest spines. Those at top and sides are also active, for the

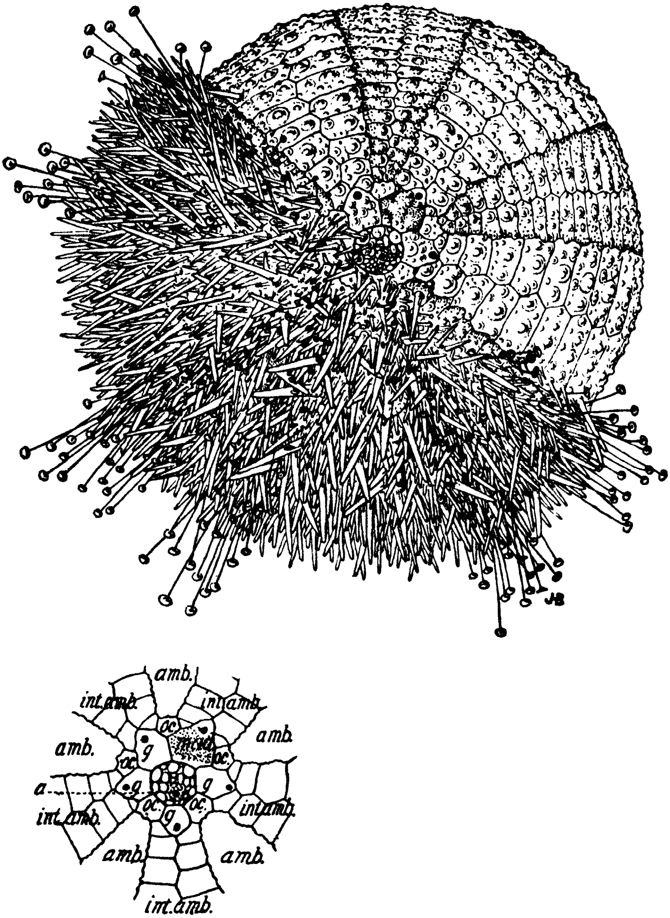


FIG. 89. — The common sea urchin, *Strongylocentrotus dröbachiensis* Say, from the coast of Maine. Entire individual, dorsal view (with spines, etc., removed from half of the shell (test)). Below is the central dorsal area with ornamentation omitted. *a*, anus, the large black spot within the periproct (the area within the circle of genital plates and protected by many small plates); *amb.*, ambulacrum; *g*, genital plate at tip of each interambulacrum, perforated by the genital opening, — the large black spot; *int. amb.*, interambulacrum; *mad.*, madreporite; *oc.*, ocular plate at tip of each ambulacrum.

urchin lives among rocks and can hence use all of its feet. Between each set of two ambulacra are the *interambulacra*, broad, spine-bearing areas composed of two columns of plates. The water-vascular system is similar to that of the starfish, except that the radial canals giving off the tube-feet lie within, not without, the test.

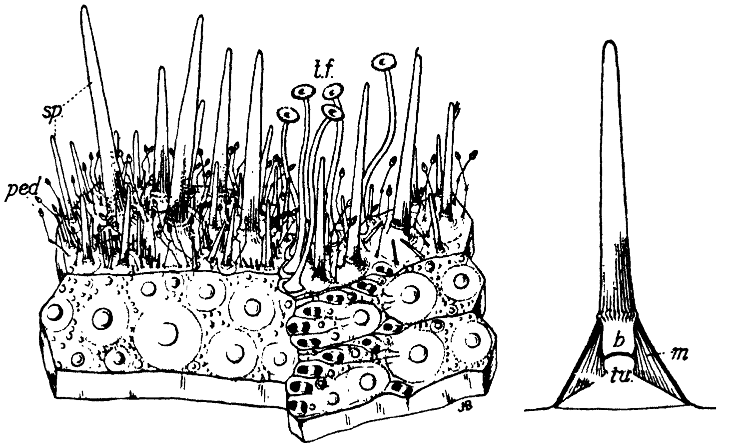


FIG. 90. — An enlargement of a small portion from Figure 89. *A*, an enlargement of the seventh and eighth interambulacral plates, and the adjoining ambulacral ones, counting from the first ocular to the right of the madrepore. *B*, a single spine (× 5), showing its ball-and-socket joint and the attachment of the muscles to move it. *b*, base of spine; *m*, muscles to move the spine; *ped.*, the small grasping pedicellariæ with the minute pincer-like heads; *sp.*, large and small spines; *t.f.*, tube-feet ending in suckers and capable of expansion to double the length shown here, or of contraction to far within the spines; *tu.*, tubercle.

Growth takes place by the increase in size of the plates and by the addition of new plates dorsally at the ends of the ambulacra and the interambulacra.

A complicated apparatus, called *Aristotle's lantern*, is connected with the digestive system. It consists principally of five enameled teeth meeting in a point; they project slightly out of the mouth, and are moved by a complicated set of muscles.

The teeth and muscles are supported by five pyramidal plates which with their connections form the skeletal part of Aristotle's lantern. (Aristotle compared this skeletal part to a ship's lantern.) These teeth are used to grind the food into bits. A wide digestive tube extends from the mouth in the center of the ventral (lower) surface to the anus in the center of the dorsal (upper) surface, winding around the inside of the test. There is no such differentiated stomach, nor are there such radial divisions of the digestive system as occur in the starfish.

The five double rows of long, slender tube-feet enable the animal to cling to the rocks over which it slowly glides in search of the algæ and small organisms on which it lives. Sea urchins are usually vegetable feeders.

Respiration is effected mainly by the upper end of the digestive canal and by the shrub-like gills at the ventral margin of the test.

The *nervous system* is similar to that of the starfish, and there are present, likewise, five eye spots at the tips of the ambulacra in the ocular plates.

The sexes are in separate individuals. At the tip of each interambulacrum is a genital or basal plate in which are openings for the extrusion of the *reproductive* elements. Through these pores the eggs and spermatozoa are cast out into the water during summer, where after union they rapidly develop into tiny translucent bilateral larvæ. The larvæ swim about and feed on smaller creatures for several weeks, each finally developing a minute, globular, radial sea urchin at the posterior end. In a few hours the larval portion becomes absorbed and leaves the minute sea urchin to drop to the sea bottom.

Strongylocentrotus dröbachiensis is found in the deep waters of Long Island Sound, in shallow tide pools north of Cape Cod, and covering the rocks upon the Maine coast. It extends into the Arctic Ocean and occurs also on the north Pacific coast.

1. Sketch (*a*) side view, (*b*) ventral view, (*c*) dorsal view. Label ambulacra, interambulacra, mouth, anus, teeth if present, openings for tube-feet, madreporite, ocular and genital plates.
2. Compare it with a starfish.

3. How and what does Strongylocentrotus eat?
4. Describe its respiration.
5. How does the animal move? How does it increase in size?
6. Of what use are the spines? Make a sketch illustrating how they are moved.

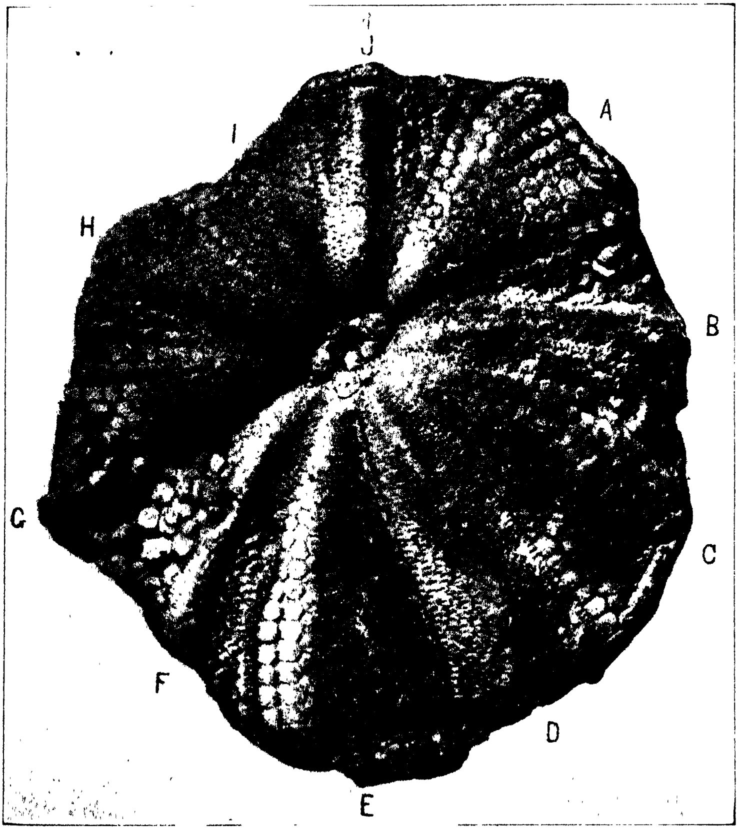


Fig. 91. — The Paleozoic sea urchin, *Melonechinus multiporus* (Norwood and Owen) which was very abundant in the shallow seas covering much of Missouri during the St. Louis (Upper Mississippian) time. Dorsal view; slightly reduced in size. *A*, *C*, *E*, *G*, and *I* are the interambulacra; *B*, *D*, *F*, *H*, and *J* the ambulacra. At the tips of the interambulacra are the genital plates, each with three pores: the ocular plates at the tips of the ambulacra are much smaller than the genitals. (From Jackson.)

7. In what directions may a spine be moved?
8. Can Strongylocentrotus climb?
9. Give the geologic range of Echinoidea.

Melonechinus multiporus (Fig. 91). *Mississippian.*

Test is very large, spheroidal, melon-like; marked vertically by elevated ribs, which are due to the thickening of the plates and are hence hardly recognizable in internal molds. Ambulacra broad with ten columns of plates at widest part; interambulacral areas with eight or nine columns of plates. Tubercles small, numerous; spines minute, needle-like. This species was very abundant in the St. Louis (Mississippian) seas of Missouri.

The earliest species of Melonechinus had fewer columns of plates than the later ones. (This genus was formerly called Melonites.)

1. Sketch the side view, noting ambulacra, interambulacra.
2. Was the living animal attached or free?

Hemiaster (Fig. 92). *Cretaceous to Recent.*

Test is elongate, heart-shaped, with mouth anterior and beneath, and anus at the posterior upper angle; it is thus

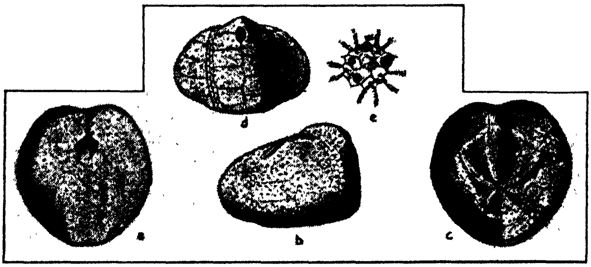


FIG. 92. — *Hemiaster parastatus* (Morton) (× ⅞) from the Upper Cretaceous of the Atlantic and Gulf regions. Showing lower (*a*), lateral (*b*), upper (*c*), and posterior (*d*) views, and the adoral area (*e*) enlarged. (After Clark.)

bilaterally symmetrical. The two posterior ambulacra are short and separated from the three larger anterior ones; the most anterior ambulacrum lies in a shallow groove.

This genus belongs to the order of spatangoids (heart-urchins), in which the jaws are lost and the necessary nutriment is derived from the oozes of the sea floor as the animal scoops up the mud in its forward movement.

1. Sketch dorsal and ventral views, noting ambulacra, mouth, and anus.

CLASS G. HOLOTHUROIDEA (SEA CUCUMBERS)

Free, with elongated, more or less cylindrical body. Mouth and anal opening at opposite ends. The body differs from that of the starfish in being greatly drawn out in the direction of the line joining mouth and anus; this line is likewise the direction of movement. The ventral surface is parallel with the axis joining mouth and anus, not at right angles to it as in the starfish, and is furnished with rows of well-developed, functional tube-feet. The place of tube-feet on the dorsal side is taken by papillæ lacking suckers. Ten large, branched, contractile tentacles, which are probably enlarged tube-feet, surround the mouth. The surface of the body turned toward the sea floor is always the same and is usually flattened. After the manner of some worms, holothurians devour sand and mud, deriving their nourishment from the organic particles contained in them.

The leathery body is usually supported only by scattered calcareous spicules of various shapes, and possesses no true skeleton. Usually the spicules alone are capable of preservation as fossils; these are known from the upper Paleozoic to the present, but representatives showing the impression of the entire body have been described likewise from the Middle Cambrian of British Columbia.

Holothurians are widely distributed at present through all seas, with a habitat extending from shallow to deep water, in tide pools, on rocks, or in the sand or mud.

Derivation of name. — Greek *holothourion*, a water-polyp, + *eidos* (*oid*), form.

Evolution of the Echinodermata

Because of their free-swimming, bilateral larvæ, echinoderms are supposed by most zoölogists to have evolved from some worm-like (possibly "round worm") descendant of the cœlenterates; or possibly from the bilateral stage that gave rise to the cœlenterates. A bilateral symmetry (usually with body flattened and with mouth and anus widely separated), accompanied by absence of radial symmetry in either food grooves or calyx plates, is seen in the early cystoids of the order Amphoridea (Cambrian-Silurian); these are usually attached to the sea floor by a short weak stalk; they are seldom free. With fixation a radial symmetry tended to develop in all plastic lines, since fixation necessitates a radial method of feeding. Moreover, when supported by a narrow stem, the form is subject to the same kind of gravitative pull as are trees, and this would tend to accentuate the development of a radial symmetry. The number of radii tended, for some as yet unknown reason, toward five.

Of the fixed classes the cystoids are the most primitive and did not survive the Paleozoic, as was likewise the case with the blastoids, with their limited area for the collection of food. The crinoids, profiting from their elongate and much branched arms, were the most successful group.

Three lines of development, the starfish, brittle stars, and sea urchins, show kinship with the Edrioasteroidea of the cystoids, and took again to a free existence. Their radiate structure shows little change in response to this new method of living except in one group of sea urchins, the spatangoids. This group developed a very distinct new bilaterality, with mouth and anus widely separated. The sea cucumbers likewise show a very early development, either from the common bilateral ancestors or from a later sessile stock. They became worm-like, with mouth and anus at opposite ends of the elongate body, with a consequent slight development of skeletal plates.

Echinoderms as Rock-Builders

Animals that can move about freely are rarely important rock-builders. Of the unattached classes of the echinoderms, — starfish, brittle stars, sea cucumbers, and sea urchins, — only the last, with their large skeletons consisting of firmly anchylosed plates, make any distinct contribution to the strata of certain areas. In the formation of the St. Louis (Mississippian) limestone of the eastern Mississippi Valley Region, the large Melonechinus assists considerably. Sea urchins also aid, at times to a large extent, in the formation of strata in the Jurassic, Cretaceous, and Tertiary. Of the fixed classes, the cystoids and blastoids are generally not of sufficient abundance to be important, though some Ordovician and Silurian strata contain many cystoids, and some Chester (Mississippian) strata many blastoids. The crinoids, with their long stems and branching arms, are very important rock-builders. Crinoidal limestones are known from the Ordovician to the Cretaceous, varying in thickness from a few feet to several hundred feet. In Germany the Trochitenkalk of the Middle Triassic (Muschelkalk) is largely a crinoidal limestone. In the Lower Pennsylvanian (Upper Rundle) of Alberta there is a stratum 200 feet thick in which there is hardly any other fossil or sediment than separate crinoid joints. Such limestones are likewise abundant in the Silurian of the Isle of Gotland, in the Niagaran of Anticosti, New York, and Wisconsin, usually in the stratified beds beyond the organic portion of a coral reef. It has been suggested that such great masses of crinoids are due to fixed species which have been torn up from the bottom of shallow seas in great storms or to freely floating species which have been blown into shallow bays, and have there died from insufficient oxygen and have sunk to the bottom. Later as such animals decayed, the stem and calyx plates were scattered by the waves.

1. Divide the phylum into classes and all minor subdivisions, giving an example of each.
2. What common characteristics do these classes possess that determine their inclusion in one phylum?

3. How do the Echinodermata differ from the Cœlenterata in the following characters: (*a*) habitat, (*b*) protecting and supporting skeleton, (*c*) locomotion, (*d*) food, (*e*) its capture, (*f*) its intake, (*g*) digestion, (*h*) circulation of body fluids, (*i*) excretion of waste, (*j*) respiration, (*k*) nervous system, (*l*) sense-organs, (*m*) reproduction, (*n*) geologic range?

4. Compare the arms of a starfish with corresponding structures in the other classes.

5. In what class would you look for the ancestor of the stalked forms?

6. In what respects do the Echinodermata show advance over the Cœlenterata?

7. What is the probable cause of radial symmetry in echinoderms?

8. Discuss briefly the evolution of the Echinodermata.

9. What classes are important as rock-builders? Give examples.

CHAPTER XI

PHYLUM X. MOLLUSCOIDEA

The Molluscoidea are aquatic, usually marine animals with a well-developed, generally U-shaped digestive canal. There is a tentacle-bearing ridge (lophophore) surrounding the mouth. This ridge is partly respiratory in function. A nerve ganglion is present, dorsal to the œsophagus. The soft parts of the body are supported and protected by a calcareous, corneous, or membranous covering.

Derivation of name. — Molluscoidea > English *Mollusca* + Greek *eidos* (*oid*), form. The external, bivalve shell of the class Brachiopoda bears some resemblance to the molluscan shell of the class Pelecypoda.

The Molluscoidea are divided into the following classes:

CLASS A. BRYOZOA (POLYZOA)

Type of class, *Bugula avicularia* (living) (Fig. 93).

The most common species on the Atlantic coast, from North Carolina to Maine, is *Bugula turrita.* This may be used in the laboratory in place of *B. avicularia.*

This is a colonial form, growing in tufts two or three inches long on piles or rocks on the seashore in all parts of the world. The colony (*zoarium*) is made up of erect stems, attached by root-like fibers to the rock or other support. Each stem consists of four parallel rows of closely arranged *zoœcia*, the individual cups. On nearly all zoœcia is an appendage, the avicularium,

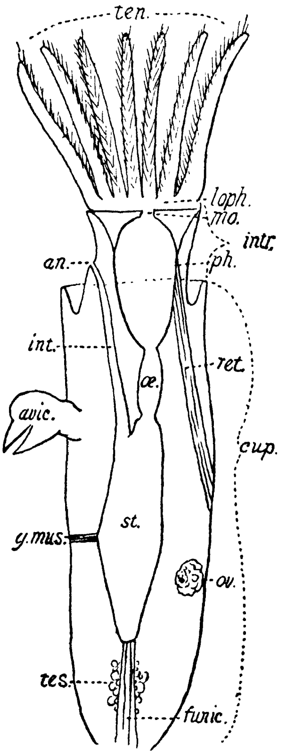


FIG. 93. — *Bugula avicularia.* Diagrammatic longitudinal section through a single individual, expanded from its protective cup of chitin, in the position of feeding. *an.*, anus; *avic.*, avicularium; *funic.*, funiculus; *g.mus.*, one of the muscles attaching the stomach to the walls of the cup; *int.*, intestine; *intr.*, introvert; *loph.*, lophophore; *mo.*, mouth; *œ.*, œsophagus; *ov.*, ovary; *ph.*, pharynx; *ret.*, one of the muscles to retract the introvert within the cup; *st.*, stomach; *ten.*, tentacles; *tes.*, testis. Much enlarged.

with very much the appearance of a bird's head, which is in almost constant movement and whose function is rather problematical, though it is doubtless somewhat protective.

Protection. — Each individual consists externally of a chitinous cup, with the broad opening extending outward from the colonial stem. (The material is closely akin to the true chitin of the Arthropoda.) This cup of chitin is the hardened and thickened cuticle of the entire animal except the anterior portion, or introvert. Into this hard-walled cup muscles can withdraw the soft-walled anterior body portion, while the contraction of the sphincter muscle at the orifice completely closes the cup and protects the inclosed soft parts. By these muscles likewise the tentacles can be swayed in any direction.

The **digestive system** is U-shaped, with mouth and anus both anterior, and is suspended within the pouch-like cœlome or body cavity of the animal. The whole anterior portion of the body, the *introvert*, has walls of thin cuticle continuous with the walls of the chitinous cup and in the contracted state of the ani-

mal it is folded back within the cup like the turned-in finger of a glove. When, however, the animal expands, the introvert is pushed out through the opening of the chitinous cup. In this expanded condition, the position of feeding, the mouth is seen to occupy the anterior end of the introvert; it is surrounded by a circular ridge, the *lophophore*, bearing about 14 tentacles. The tentacles surrounding the mouth are densely covered with cilia on their inner surfaces and the vibration of these cilia drive currents of water towards the mouth. The particles of food in these water-currents, as well as those caught by the prehensile tentacles, pass through the mouth into a wide pharynx, thence through a short œsophagus into the stomach. It is here that the digestive canal makes its U-shaped bend, for the intestine rises from the forward end of the stomach and extends in an anterior direction, near and parallel to the œsophagus, to its termination in the anus, which is near the mouth, but outside the circle of tentacles.

There are no *blood vessels* and no *excretory organs*. The digested food passes through the digestive canal into the pouch-like body cavity (cœlome), which contains a fluid in which are colorless corpuscles, the leucocytes. The movement of this fluid is effected largely by the movements of the animal. The collection of the nitrogenous waste matter is probably carried on chiefly by these leucocytes.

The tentacles are the chief organs of **respiration**; they are hollow, forming narrow prolongations of the cœlome, and probably effect a transfer of the fresh oxygen of the sea water for the effete gases of the body cavity.

No central **nervous system** has been traced in Bugula. In some other genera it takes the form of a small, rounded ganglion between the mouth and the anus which gives off nerves to various parts of the body. Aside from the tentacles, which may be organs of touch, there are no organs of special sense in any of the Bryozoa, except possibly the *epistome* of the Phylactolæmata; this is a fold of the lophophore which closes the mouth and may in a manner taste what passes into the mouth.

Each zoœcium is lined internally by a cellular substance, the parenchyme, and through this parenchyme it is posteriorly closely united with its neighbors.

Reproduction. — Each new colony arises from a sexually produced individual. The same zoöid possesses both ovary and testis formed from specially modified cells of the parenchyme. The spermatozoa move about in the cœlome and there fertilize the ova. The fertilized ovum passes into a rounded outgrowth of the zoœcium, which forms a sort of brood pouch (oœcium or ovicell) and there develops into the embryo. This escapes from the parent body, swims about a few hours, and then becomes fixed by a sucker to some object, and subsequently gives rise asexually by budding to the new adult branching colony.

1. Examine a colony, noting its attachment, method of branching, the individual cups, avicularia.
2. Examine the mounted specimen under a compound microscope, noting the U-shaped digestive canal, tentacles surrounding the mouth, the chitinous cup.
3. What is the habitat of Bugula?
4. How is it protected?
5. How does an individual get its food?
6. Describe the method by which the digested food reaches all parts of the animal.
7. How does it breathe?
8. How are the individuals of a colony united?
9. Describe its method of reproduction.
10. What would a fossil Bugula look like?

General Survey of Class Bryozoa

Usually colonial and incrusting animals. A tentacle-bearing ridge, lophophore, surrounds the mouth. An introvert is usually present, and a U-shaped digestive tube. The two sexes are commonly united in the same individual. The body wall of each individual, called the zoœcium, usually becomes hard by means of horny or calcareous materials, forming an exoskeleton which persists after the death of the animal, and which forms the only portion of the animal capable of being preserved

in the fossil state. Even the remains of the larval stage (protœcium), a minute circular pit, is usually preserved. The first bud of the protœcium is known as the ancestrula; this buds off other zoœcia, which in turn repeat the process, thus building up the colony.

Although the individual zoœcia are usually less than one millimeter in diameter, the colony (zoarium) may reach a length of 30 centimeters or more, a size sufficient to render them desirable as food, were it not for their heavy chitinous or calcareous walls. The zoaria of both fossil and recent forms are usually perfect, showing rarely any injury, thus indicating that they seldom serve as food, though certain birds and fish have been known to eat them.

Most Bryozoa live in comparatively shallow water; they are known from the Lower Cambrian to the present.

The hard parts of bryozoöns differ from those of corals in the absence of cœnenchyme, the presence of oœcia in the walls, the minute size of the zoœcia, the absence of septa, and the presence of the protœcium (in corals there are no embryonic hard parts).

Derivation of name. — Bryozoa > Greek *bryon*, moss, + *zoon*, animal. The colonies frequently look like tufts of moss. The name preferred in England is Polyzoa (Greek *polus*, many, + *zoon*, animal). The many individuals formed by budding remain united in a colony.

Bryozoa are subdivided into the following subclasses and superorders:

1. Ectoprocta
   a. Gymnolæmata
   b. Phylactolæmata
2. Entoprocta

SUBCLASS 1. ECTOPROCTA

Colonial Bryozoa with the mouth inside but the anus outside the tenacle-bearing lophophore (whence the name from Greek *ektos*, outside, + *proktos*, the anus). A well-developed introvert is present. Body wall is membranous or calcified.

SUPERORDER *a*. GYMNOLÆMATA

Almost exclusively marine; lophophore circular; epistome absent (whence the name from Greek *gymnos*, naked, + *laimos*, the gullet). At present the marine forms live from tide level to a depth of over 18,000 feet. Geologically they extend from the Lower Ordovician to the present. All fossil Bryozoa known, with possibly a single exception, belong here.

The Gymnolæmata are divided into five orders:

Ctenostomata. — Zoœcia horny or membranous, isolated, budding from internodes of the tubular stolon. Poorly represented from the Ordovician to the present.

Cyclostomata. — Zoœcia simple calcareous tubes, usually without transverse partitions. Ordovician to present. (Example, Hederella.)

Trepostomata. — Colonial, massive; zoœcia round or polygonal tubes, floored at intervals by tabulæ. Walls thickened, at times with cysts (Cystiphragma). Since the mature portion of the wall is distinctly thicker than the earlier portion, the name of the order is from Greek *trepos*, changed. The zoœcia separate upon fracture and in other respects look much like such tabulate corals as Favosites, but the characters of the primary individual of the colony are bryozoan. Paleozoic. (Example, Monticulipora.)

Cryptostomata. — Colonial; zoœcium with a short early portion, above which it continues in the mature part as a thickened tubular shaft, with a round opening. Paleozoic. (Example, Fenestella.)

Chilostomata. — Zoœcia of various forms arranged side by side; the opening placed anteriorly, usually smaller than diameter of zoœcium but often appearing to occupy the entire diameter, owing to the non-calcification of the front wall and its removal in fossilization. Polymorphism occurs; some polyps become avicularia, etc. Jurassic to present. These are the dominant bryozoöns since the Upper Cretaceous. (Example, Membranipora, Bugula.)

Hederella (Fig. 94). *Devonian.*

Attached zoaria, with tubular zoœcia given off on alternate sides from a central tubular axis.

Sketch a colony. Label zoœcia, tubular axis.

Monticulipora (Fig. 95). *Ordovician to Silurian.*

Colonial, occurring as a flat expansion of upright, parallel tubes of calcium carbonate. These tubes have thick, non-

porous walls and are divided into compartments by numerous transverse partitions (diaphragms). The lowest portion of each tube is the narrowest, having been built by the individual in its youth ; from this point the tube rapidly enlarges to its maximum, normal diameter. The diaphragms mark its withdrawal from a lower to a higher position. Unlike Bugula, each tube

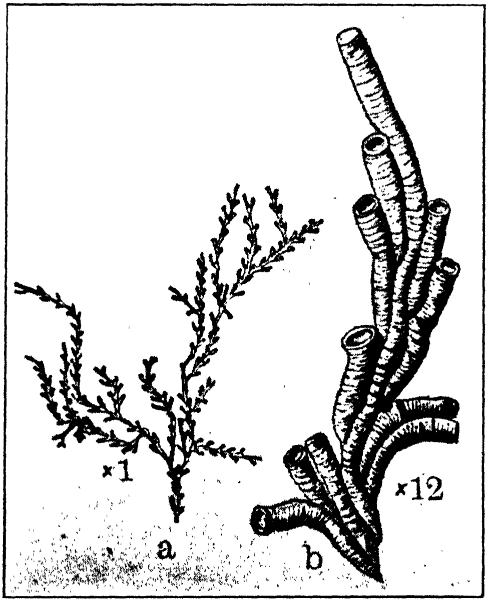


FIG. 94. — *Hederella canadensis* (Nicholson) from the Middle Devonian of eastern North America. (After Hall and Simpson.)

increases in length throughout life. Since, however, the soft parts of the animal increase in size but little, the lower (older) portions of its house-like skeleton must be vacated ; this removal takes place at more or less regular intervals, probably due to a contraction of the soft parts of the body following the extrusion of the sexual elements, and wherever the base of the body comes to rest it secretes a calcareous plate, the diaphragm. The tube openings are polygonal or rounded. The surface of the colony

is often made irregularly rough by the elongation of groups of individual tubes so as to form small elevations, monticules (whence the name from Latin *monticulus*, little hill, + *porus*, a pore).

1. Sketch (*a*) an outline of the entire colony, (*b*) a view of three zoœcia showing both the tubes and their openings, also diaphragms in one. Label zoœcia, diaphragms.
2. What is the probable cause of the diaphragms?
3. How do the zoœcia differ in composition from those of Bugula?

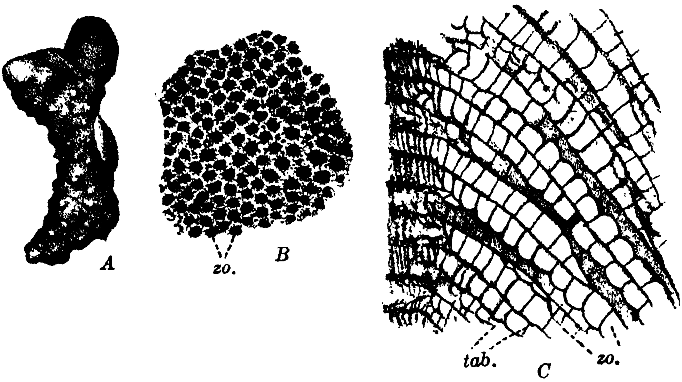


FIG. 95. — *Monticulipora arborea* Ulrich, from the Middle Ordovician of Minnesota. *A*, portion of a colony, natural size. *B*, view of surface (× 9), showing the cups (zoœcia, *zo.*) occupied by the soft bodies of the individual animals during life. *C*, longitudinal section from the periphery of branch inwards through fifteen corallites (× 18); *zo.*, zoœcia; *tab.*, tabulæ or diaphragms. (From Ulrich.)

4. Indicate in one zoœcium the position last occupied by the soft portions of the animal.
5. How does such a bryozoön as Monticulipora resemble a coral like, for example, Favosites (Fig. 73)? How do they differ?

Fenestella (Fig. 96). *Silurian to Permian.*

Colony usually funnel-shaped, composed of a calcareous net-like frame-work made up of straight radiating branches united by cross bars (whence the name from Latin *fenestra*, a window, + the diminutive ending *ella*). Upon the upper (inner) side of the radiating branches are two rows of small pits

(zoœcia), separated by a median keel-like ridge; each of these pits lodged the soft body portion of an individual bryozoön. The cross bars do not bear pits. In development the large first, or primary, cup (protœcium) secreted by the sexually produced

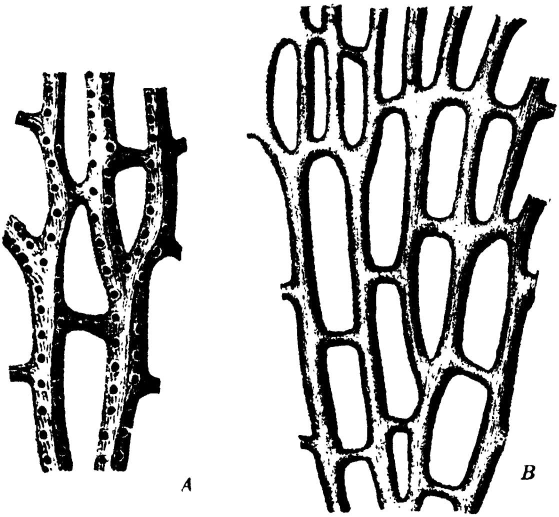


FIG. 96. — *Fenestella filistriata* Ulrich, from the Burlington limestone (Mississippian) of Iowa. *A*, inner surface of a colony showing the two rows of zoœcia. *B*, outer surface of a colony; note absence of zoœcia. Each × 6. (After Ulrich.)

zoöid budded off two cups; each of these gave rise to others. Continued budding produced the mature colony.

1. Sketch the upper side of a portion of a colony; indicate the zoœcia, median ridge, cross bars.
2. Sketch in outline the probable shape of the entire colony.
3. Outline its development.
4. What is the significance of the name?

Membranipora (Fig. 97). *Jurassic to present.*

This genus differs from Bugula in the arrangement of the individuals in the colony. The colony has the form of a flat expansion, incrusting seaweed; thus the zoœcia, the individ-

uals, are arranged in one plane, irregularly, or in rows. Each individual, as in Bugula, consists of a chitinous bag, but much shorter and with the rim around its aperture calcified. These

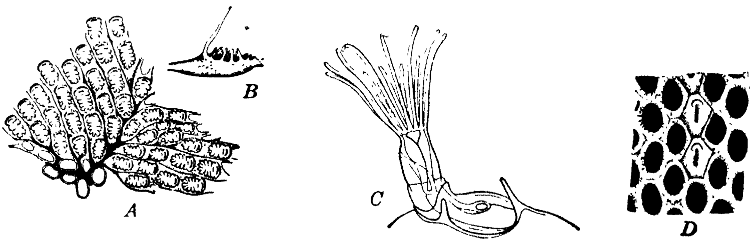


FIG. 97. — The marine bryozoön, Membranipora. *A*, *M. pilosa* (× 15) from the coast of Massachusetts. Portion of a colony seen from above. *B*, single cell of same seen in profile. *C*, same with one of the individual animals expanded as in feeding. *D*, a fossil species, *M. rimulata* Ulrich (× 10), from the Eocene of Maryland. (From Ulrich. *A–C* from Verrill and Smith.)

individual zooecia are united to one another by their thickened walls to form a flat, net-like framework.

1. Sketch three zoœcia of a dried specimen.
2. How many individual animals do these three represent?
3. How do the zoœcia differ from those of Bugula?
4. Of what is the skeleton composed?
5. Where at present may living Membranipora be found?
6. What conditions must exist for such a living form to be preserved as a fossil?

SUPERORDER *b*. PHYLACTOLÆMATA

Fresh-water inhabitants; lophophore horseshoe-shaped; an epistome overhangs the mouth (whence the name from Greek *phylassein*, to guard, + *laimos*, the gullet). Unknown in the fossil state, with the possible exception of Plumatellites from the Cretaceous of Bohemia.

SUBCLASS 2. ENTOPROCTA

Colonial or solitary Bryozoa with both mouth and anus within the circular, tentacle-bearing lophophore (whence the

name from Greek *entos*, within, + *proktos*, the anus). The body wall is not calcified. The introvert is but slightly developed or absent. The half-dozen genera belonging to this small subclass are marine, except the American fresh-water genus Urnatella. Not known in the fossil state.

CLASS B. BRACHIOPODA (BRACHIOPODS)

Type of class, *Terebratulina septentrionalis* (living) (Figs. 98, 99).

This species is abundant off the coast of Maine, living from low tide to a depth of 300 feet. It occurs from Massachusetts to Nova Scotia inclusive. (Species of the same genus occur in the shallower waters of nearly all seas.)

The animal is protected by a calcareous shell, usually five-eighths of an inch long and consisting of two pieces (*valves*). It is attached to a rock or other support by a posterior, fleshy prolongation of the body, called the *pedicle.*

Skeleton. — The valves are secreted by two fleshy folds of the body, the mantles. The pedicle passes out through a hole (the *pedicle opening* or *delthyrium*) in the beak of the larger or ventral valve; hence this valve is at times called the *pedicle valve.* Fastened to the inside of the smaller or dorsal valve is a calcareous ribbon-like loop, the *brachidium,* forming an internal support for the hollow, arm-like branches (*brachia*) of the lophophore; because this valve supports the brachia it is often called the *brachial valve.*

Externally the shell is marked by *concentric lines* (growth lines) which represent the successive stages of growth; as the shell grew, new layers were added to the inside, projecting beyond the preceding layers and forming thus a series of shell extensions. Since the pedicle is present in the youngest shell-secreting stage of the brachiopod, and the animal when young must have had a minute pedicle, growth must have begun at the small end or *beak* of the shell. That this was the initial point of growth is seen likewise by the curving of the growth lines

around it. The beak, then, is the oldest portion, while the latest built portion is the edge of the shell away from the beak.

The pedicle is further inclosed, as it passes out of the valve, by two triangular plates, the *deltidial plates*, which, therefore, more or less close the delthyrium. A pair of teeth on the posterior portion of the pedicle valve fit into corresponding sockets in the brachial valve; these sockets are also the bases of the calcareous skeleton that supports the arms. Projecting between the teeth of the pedicle valve is a short prolongation, the *cardinal process* (*c.p.*, Fig. 98, *A*) of the posterior portion of the brachial valve.

Since during the growth of the shell the teeth enlarge externally and anteriorly, while probably both resorption and wear take place internally and posteriorly, the hinge line becomes continually broader; *i.e.*, the teeth move farther apart and, *pari passu*, calcium carbonate is added to the inside of the sockets, thus causing the hinge line of this valve likewise to become broader. Thus the brachial valve as a whole moves anteriorly.

Muscles. — The valves are opened and closed by muscular action. The pedicle valve may be said to be stationary because to it is firmly attached the pedicle. Two pairs of muscles, the *diductors*, extend from the posterior portion of the pedicle valves back to the tip of the cardinal process. Being thus situated, their contraction tends to cause the valves to fly open. The valves close by the contraction of two other muscles, the *adductors*, which pass transversly from valve to valve. These are elongate and narrow on the pedicle valve, and in passing over to the brachial valve divide, leaving here four more or less circular scars. A pair of muscles extending from the brachial valve and another pair from the pedicle valve with insertion on the pedicle enable the animal as a whole to move in many different directions.

The soft body wall gives off two folds or *mantles*, one fitting closely to and secreting the pedicle valve, the other secreting the brachial valve. Prolongations of this mantle, the cæca, fitting

into minute pores (tubules) in the valves, probably supply nourishment to and take waste from the non-calcareous part of the shell. Any marked injury to a mantle is necessarily

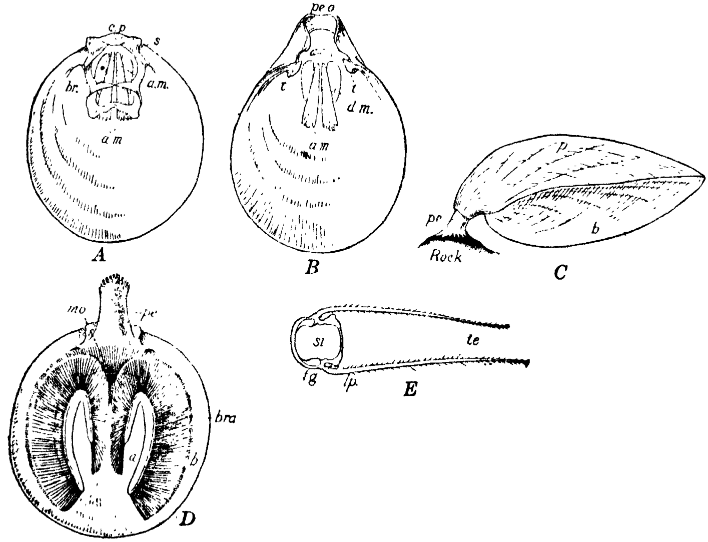


FIG. 98. — *Terebratulina septentrionalis* Couthoy, from the coast of Maine. *A*, inside of the brachial valve. *B*, inside of pedicle valve. *C*, side view of the animal fastened to a rock by the fleshy pedicle. *D*, soft body of animal in brachial valve with pedicle valve removed. *E*, an enlarged section of the brachium along line *a–b* in *D*, showing the ciliated tentacles (*te.*) which urge the food into the ciliated food grooves (*f.g.*); *a–b*, line of section, *E*; *a.m.*, abductor muscle scar; *b*, brachial valve; *br.*, brachidium; *bra.*, the horseshoe-shaped lophophore with its branches or arms, — the brachia; *c.p.*, cardinal process, place for the attachment of the diductor muscles; *d.m.*, diductor muscle scar; *f.g.*, food groove; *lp.*, lip; *mo.*, mouth; *p*, pedicle valve; *pe.*, pedicle; *pe.o.*, pedicle opening for passage of pedicle; *s*, socket into which fits the tooth (*t*); *si.*, sinus; *t*, tooth; *te.*, tentacles. All natural size, except *E*.

reflected in the shell. If something injures a mantle edge, the first process in healing is a puckering up of the mantle around the injured place (as in the healing of an injury to a man's skin) which causes a like puckered appearance in the shell at that place; as the mantle becomes healed, the growth lines of the

shell become more and more regularly spaced. But since an injury to one mantle causes a lessened vitality, even if very slight, of the entire animal, the opposite mantle likewise displays a crowding and general interruption of regularity in the growth lines. It thus follows that the life history of the individual can be read from the beak forward, not only in relation to the shape and size of the shell, but to its injuries, social crowdings, and general health. (See also Fig. 14.)

Most of the inner space between the mantles is divided transversely into two parts by a membrane. The anterior part is filled with the tentacle-bearing lophophore; the posterior contains the visceral cavity, with the alimentary canal and the sexual organs. The lophophore is supported by the calcareous ribbon, the *brachidium;* those portions which diverge arm-like from the two sides of the mouth are called the *brachia.*

The **food** consists of diatoms, infusorians, etc., as well as of microscopic organic fragments. Upon each branch of the brachia there is a groove bounded on each side by lines of ciliated tentacles, which extend from the tip of each arm to the mouth, a slit-like opening in the middle of the lophophore.

The motion of the cilia upon these tentacles and within the food grooves (Fig. 98, *E*) causes a current of water, and with it any near-by food particles, to sweep into the grooves and along these grooves to the mouth.

From the mouth the food passes through an œsophagus into the stomach, into which from each side opens a large gland which probably performs the functions of both liver and pancreas of higher forms, thence into the intestine which terminates in a closed point, no anal opening being present (Fig. 99, *F*). The *digestive waste,* in the shape of minute pear-shaped bodies, is carried out of the stomach through the œsophagus by the cilia lining it, and is ejected through the mouth. The digested food absorbed by the surface of the digestive tract, aided very largely by the stomachal glands, passes into the body cavity surrounding it. The fluid filling this body cavity is moved by the cilia lining it and performs the function of the blood;

thus the digested food entering it is urged into all parts of the body. This body cavity, or cœlome, is continued into the lophophore and its branches; it also extends into each of the mantle lobes in the form of branched canals, *pallial sinuses;* the impression of these upon the shell is often seen in fossil forms (Fig. 111, *D*, *E*). The cœlomic fluid or blood is colorless and contains corpuscles.

The *excretory organs* consist of two large funnel-shaped nephridia, one on each side of the intestine. They have a wide inner opening into the cœlome and a narrower outer opening near the mouth; their function is to get rid of the nitrogenous waste gathered from the cœlomic fluid.

Respiration is effected mainly through the mantles, for the blood sinuses branch broadly within them; it is largely aided also by the lophophore and its tentacles.

There is a **nerve** ring around the œsophagus enlarged into a dorsal and a ventral ganglion which give off nerves to the lophophore, mantle, etc. No sense organs are known, but the animal is sensitive to touch.

The **sexes** are separate. After the *fertilization* of an ovum by a spermatozoön, the single cell divides into two cells. Repeated division results in the formation of a many-celled but hollow sphere, the blastula; one side of this sinks in against the other, producing a two-walled cup, the gastrula. After the cup-like opening of the gastrula closes, the embryo becomes ciliated and is capable of moving freely about. It now becomes gradually constricted into three regions, the head, thoracic and pedicle areas, with a total length of about a third of a millimeter. From the middle, or thoracic, segment grows a ring-like fold extending back towards the pedicle segment. Soon, however, this circular fold or mantle divides into two, the dorsal and ventral mantle lobes, which develop bundles of chitinous bristles upon their free edges. After six to twelve days of this early embryonic life, the animal settles down, attaching itself to some foreign object by the end of the mucus-coated, sucker-like pedicle; later the mantle lobes turning inside out, bend forward

so as to inclose the head segment and what is now the outer surfaces secrete the dorsal and the ventral valves of the horn-like, embryonic shell (*protegulum*, Fig. 99, *G*, *H*, *I*). About the same time a crescentic fold, the future lophophore, grows out from the inner side of the brachial mantle lobe, developing gradually into the two arms which diverge from the mouth; simultaneously the muscles develop, the additions to the shell

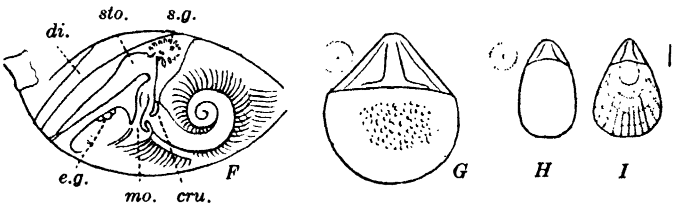


FIG. 99. — *Terebratulina septentrionalis* from the coast of Maine. *F*, longitudinal vertical section through entire animal; *G*, *H*, *I*, young stages of the shell, looking upon the brachial valve and the pedicle opening of the pedicle valve. *G*, earliest attached stage in the growth of the shell, showing the large open delthyrium. *H*, a later stage. *I*, stage showing the introduction of the radiating striæ and an approach to the adult in outline. *cru.*, crura (the bases of the brachidium); *di.*, diductor muscle; *e.g.*, external glands; *mo.*, mouth; *s.g.*, stomachal glands; *sto.*, stomach. The sizes of *G* and *H* are indicated by the mark within the circle, of *I* by the line to the right. (From Morse.)

become calcareous, and in all ways the animal approaches the adult.

1. Examine specimens, noting pedicle, mantle, adductor and diductor muscles; the relation of mouth to food grooves on lophophore.

2. Sketch transverse section of one of the brachia, labeling food groove and tentacles.

3. Make drawings of (*a*) entire shell, side view, (*b*) interior and exterior of each valve. Label pedicle and brachial valves, pedicle opening, teeth, sockets, cardinal process, brachidia, adductor and diductor muscle scars.

4. Sketch an ideal longitudinally transverse section through the slightly gaping valves, labeling the valves, pedicle opening, cardinal process, muscles and mantle.

5. How are the valves held together? How are they opened? How closed?

6. Give the habitat of *Terebratulina septentrionalis.*
7. What does the animal eat? How does it procure its food?
8. Briefly describe its digestion; absorption; circulation.
9. How is the digestive waste thrown off?
10. How does the animal breathe?
11. What is its nervous system like?
12. Describe the development of an individual from the fertilized egg to adulthood.

General Survey of Class Brachiopoda

Marine animals, secreting a bivalved, equilateral, inequivalved shell, which is composed of lime carbonate, lime phosphate, or a horny substance (ceratin); the valves are dorsal and ventral in position. The animal, in its youth, is always attached to a foreign object by a posterior, fleshy stalk, called the pedicle; when adult the pedicle may be lost, but in all such cases the animals are held in place by social crowding, spines, or other devices (Rafinesquina, *Stropheodonta demissa*, Productus); at times the shell is cemented to some foreign object (Crania, Meekella, Richthofenia).

The valves are opened and closed by muscles, the impressions of which show upon the interior of the valves in front of the beaks (Fig. 98, *A*, *B*).

The interior of the shell is lined by the mantle, a membranous fold of the body-wall, which is often studded with minute tubes, the cæca; these fit into correspondingly minute holes (tubules) in the shell; the tubules give to the shells their *punctate* appearance; in some species, as *Terebratella plicata*, this is quite coarse, being almost visible to the naked eye. Within the mantle are hollow spaces, the pallial sinuses; impressions of these sinuses are often found upon the interior of the valves (Fig. 111, *D*, *E*).

The pedicle valve is secreted by the ventral and the brachial valve by the dorsal mantle lobe. In those forms in which the brachial valve as a whole moves forward during the enlargement of the shell, this would leave the dorsal surface of the pedicle unprotected were it not that this surface has developed upon

it one or two special plates. In a portion of the Articulata (the Protremata) the surface of the pedicle itself secretes a shell, the *deltidium*, which unites with the posterior margin of the pedicle valve and continues to grow anteriorly (as in Rafinesquina). In the rest of the Articulata (Telotremata) where the

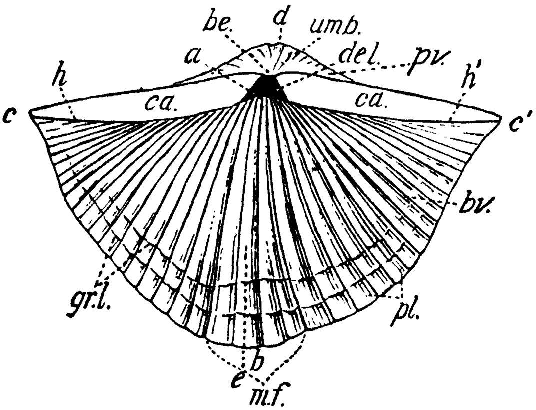


FIG. 100. — Sketch to illustrate terms describing the exterior of the brachiopod shell. (*Spirifer increbescens* Hall (× 2), from the Mississippian of Alberta.) *a–b*, length of shell (from hinge line beneath the beak to front of shell); *b*, anterior margin or front of shell; *be.*, beak, the posterior end of the shell; *bv.*, brachial valve; *c–c'*, width of shell; *c* and *c'* are the cardinal extremities; *ca.*, *cardinal area* of pedicle valve, the flattened area above the hinge line and between the cardinal extremities (each valve has a cardinal area); *d–e*, height of shell (measured between the centers of the valves and at right angles to the plane of length and breadth); *del.*, delthyrium, or triangular pedicle opening; *gr.l.*, concentric growth lines marking the anterior margin of the shell at successive periods; *h–h'*, hinge line (compare Figure 107, *h.l.*); *m.f.*, median fold (composed of four plications in this species); *pl.*, plications (folds radiating from the beak, not longitudinally striate); *p.v.*, pedicle valve; *umb.*, umbo of pedicle valve.

deltidium is absent, the extension of the ventral mantle lobe grows out laterally for the protection of that portion of the pedicle by a secretion of two plates, the *deltidial plates* (as in Atrypa).

Teeth and sockets are absent in many forms with ceratin (horn-like) shells; these are therefore known as the Inarticulata,

the opening and closing of the valves being effected by a more complicated set of muscles. In the great majority of brachiopods the shells are calcareous and bear teeth and sockets; these are the Articulata.

In the Inarticulata, where the setæ upon the mantle margins are long, acting as strainers (Fig. 101) to the ingoing water, the shells are non-plicate. In the Articulata, where the setæ are short, the shells are often plicate. In a plicate shell the valves need open but slightly to admit sufficient water and yet keep out sand, enemies, and other objectionable objects.

The pedicle valve can usually be distinguished from the brachial by some one of the following characters:

1. Larger size and greater depth.
2. Presence of a pedicle opening.
3. Higher cardinal area (vertical distance from hinge line to beak) than in the brachial valve.
4. Beak incurved over that of brachial valve.

Brachiopod shells often appear to be very similar to pelecypod shells, but may usually be readily distinguished from them by one or more of the following characters:

Brachiopoda	*Pelecypoda*
1. Equilateral	1. Inequilateral
2. Inequivalved	2. Equivalved (generally)
3. Pedicle opening present (except in Atremata)	3. No pedicle opening present (in some a byssal notch or hole)
4. Teeth in one valve, sockets in the opposite valve (except in Inarticulata)	4. Teeth and sockets in each valve (typically)
5. No ligament present; valves opened by muscles	5. Valves not opened by muscles but by ligament or resilium at hinge line
6. Valves dorsal and ventral	6. Valves right and left

It is suggestive of *retrogression* in the Articulata subclass that while in living species the intestine ends blindly, in Paleozoic forms there was probably a functional anus. In Rensselæria, Athyris, Atrypa, Rhynchonella, etc., the beak of the

brachial valve is notched or perforate (between floor of valve and union of the bases of the arm supports) for its passage to the exterior. In Strophomena and Stropheodonta it passed between the branches of the cardinal process. In living Inarticulata, as Lingula, the digestive canal ends in an open anus.

All brachiopods are in the larval stage free-swimming, sometimes for a very short time (longest among Inarticulata); it is hence during this period that their *distribution* in space takes place. The cause of the distribution is mainly one of ocean currents, since the microscopic larva, about a third of a millimeter long, swims about by a twirling motion for comparatively few hours and at a rate which could carry it only about a yard an hour.

Brachiopod shells are small, averaging an inch in length and breadth to an inch and a half. The largest species known — *Productus giganteus* of the Mississippian — reaches at times a width of almost a foot, while mature forms are known which are no larger than a pinhead.

There are about 200 species of living brachiopods, distributed in about 60 genera, only seven of which belong to the Articulata. Brachiopods were much more abundant in former periods of earth history; over 3000 species are known from the Silurian alone.

Living brachiopods are found in all seas and down to depths of 17,000 feet, hence at all oceanic temperatures; about 20 per cent live in the shallow seas around Japan, the most prolific area for these shells. Over 70 per cent live in shallow waters, *i.e.*, from between tides to a depth of 600 feet. The great majority (75 per cent) of the Inarticulata live above the 15-fathom line, while but 20 per cent of the Articulata live here. Compared with the deep-sea species, the shallow water and littoral forms are much more prolific, with much thicker and usually larger shells. Brachiopods are thus very important in the study of ancient geography. For example, the presence of fossil Inarticulata, especially those of the Lingula group, is good evi-

dence of shallow water deposits. Of those species belonging to groups existent in the Paleozoic, not one is known which at present has a wholly abyssal habitat; most of the abyssal forms date from stocks having their rise in the middle Mesozoic or later. Hence the conclusion, corroborated by other classes of animals, that abyssal seas began to form at the close of the Paleozoic with the late Paleozoic upheavals, known for North America as the Appalachian Revolution.

Though all brachiopods are strictly marine in habitat, some forms, such as Lingula, can endure a considerable amount of fresh water, living in estuaries where there are heavy spring freshets, but they never live in rivers.

The living inarticulate brachiopods possess a wonderful vitality. Lingula may be exposed between tides, covered with mud from freshets, or immersed in fetid water for months without apparent ill effects. Crania will also thrive under most adverse conditions. Such adaptability is probably the cause of the persistence of these two genera from Ordovician times to the present.

The persistence of genera and species in time varies greatly. Some genera, as Hipparionyx and Rensselæria (Lower Devonian), survived but a short time; while others, as Lingula and Crania, have existed since Ordovician times. *Rhynchotrema capax* (Richmond formation of the Upper Ordovician), for example, was short-lived but of wide distribution; it is thus a good index fossil (see page 32), while *Leptæna rhomboidalis,* persisting from mid-Ordovician to Mississippian, *Atrypa reticularis,* throughout the Silurian and Devonian, and *Productus semireticulatus,* throughout the Mississippian and Pennsylvanian, were the brachiopod Methuselahs of the Paleozoic; these forms are accordingly almost valueless as indicators of the age of their inclosing strata.

Brachiopods are known since the earliest Cambrian, and therefore the class must have originated in the pre-Cambrian; the class reaches its maximum of differentiation in the Silurian and Devonian, with the dying out of stocks in the late Paleo-

zoic. Since Mesozoic times the rhynchonellids and terebratulids have dominated, and along with them a few lingulids, discinids, cranids, and strophomenids have persisted. The class is tending slowly toward extinction.

At the end of the 17th century, brachiopods were commonly called Lampades or lamp-shells, a name whose application may be discerned if Terebratula (Fig. 110) be compared with a common design of ancient Roman lamp.

Derivation of name: Brachiopoda > Greek *brachion*, arm, + *pous* (*pod*), foot. The arms (brachia) were formerly thought to be organs of locomotion.

The Brachiopoda are subdivided into two subclasses:

1. Inarticulata.
2. Articulata.

SUBCLASS 1. INARTICULATA

Valves are held in apposition merely by muscles, there being usually no teeth or sockets to hold the two valves firmly together (whence the name from Latin *in*, not, + *articulatus*, jointed). Intestine is long, ending in an anus; this in the Lingula group opens laterally between the two valves. Shell is corneous or calcareo-phosphatic.

Lingula (Fig. 101). *Basal Ordovician to present.*

Valves thin, almost equal, elongate, tapering towards the beak (*i.e.*, tongue-shaped, whence the name from Latin *lingula*, a little tongue). Valves glistening, composed of alternate layers of phosphate of lime and a horn-like substance (ceratin), impunctate. The animal burrows in the sand by means of the long, slender pedicle which emerges from between the two valves and not through one of the beaks as in the majority of other brachiopods. The burrow is a vertical tube up to 12 inches in length, in the lower portion of which the pedicle is attached to the sand particles. By extension of the pedicle, two-thirds of the shell may project above the surface of the mud flats, but when the animal is disturbed the pedicle contracts and quickly withdraws the shell halfway down the tube.

Lingula lives between tide marks in tropical waters where the mud flats are black from decaying organic matter. Clean sand is apparently unfavorable to the growth of the animal. In southern Japan and the Philippine Islands the pedicle or the entire animal is boiled and used as food.

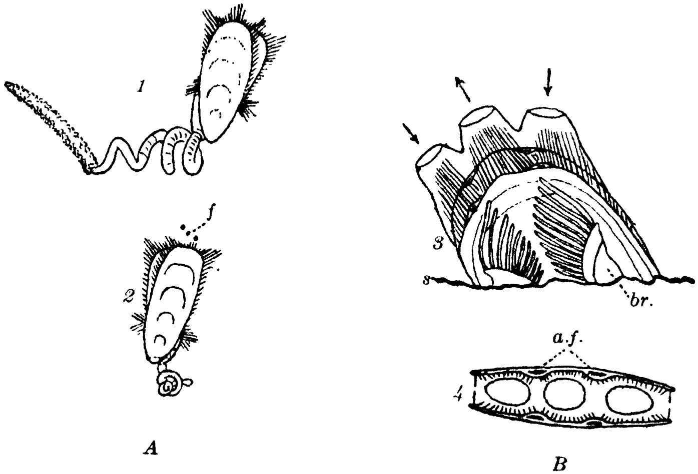


FIG. 101. — Brachiopod movements. *A*, a Lingula-like shell, *Glottidia pyramidata*, very abundant upon the shoals of the North Carolina coast, exposed at low tide. Natural size. *1*, a characteristic attitude; the sand tube inclosing the posterior end of the pedicle is here preserved. *2*, fæces (*f*) being extruded from shell. *B*, *Lingula lepidula*, very abundant upon the coast of Japan, showing the formation of tubes by the mantle and setæ. Through these tubes the water is urged by the cilia lining the brachia, and with the water food is taken in and waste is extruded by the outgoing current. *3*, attitude in sand with setal tubes formed; the brachia show through the transparent shell. *4*, front view of above. *a.f.*, anterior folds of mantle; *br.*, brachia; *s*, surface of the sand in which the animal lies half buried. (From Morse.)

Lingula anatina is a large species very abundant in the Japanese seas.

Glottidia pyramidata (Fig. 101, *A*), belonging to the Lingula group, is very abundant off North Carolina on shoals exposed at low tide; it occurs from Chesapeake Bay to Florida. In its normal condition, it lies with its shell half buried in the sand,

its anterior setæ so grouped as to form three rude channels for the entrance of water at the angles of the front of the shell and for its exit at the middle. Each mantle is at the same time raised into two folds, one upon each side of the median line of the shell, thus aiding in the formation of these water channels (cf. Fig. 101, *3*). The tentacles of the brachia are directed towards these setal tubes, while the vigorous motion of the cilia covering the tentacles causes the movement of the water. At this time the two valves are separated vertically but not laterally. Anteriorly they are open, but posteriorly as nearly closed as the pedicle will allow. The sand is kept out of the buried portion of the shell by the arrangement of the lateral setæ vertical to the plane of the valves, the setæ from opposite mantles meeting tip to tip. When disturbed the shell is quickly drawn down into the sand through the contraction of its long pedicle, the lower end of which obtains greater purchase by being sheathed in a tube of sand grains cemented together by the mucus which it secretes. This species does not live beyond a year.

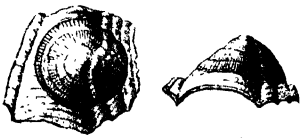


FIG. 102. — *Crania bordeni* Hall and Whitfield, from the Middle Devonian of Indiana. Natural size. *A*, an entire individual attached to a brachiopod shell which has vertical ribbing at the right of the figure. The conformation of the upper valve to the ornamentation of the brachiopod shell indicates the intimate relationship existing between the mantle edges of the two valves. *B*, side view of the same. (After Hall and Clarke.)

1. Examine specimens on the demonstration table, noting the elongate pedicle emerging from between the two valves.
2. How long geologically has Lingula existed?
3. Is either valve perforated by a pedicle opening?
4. What is the use of the long pedicle?
5. How does the animal get its food?
6. How is the sand kept out of the buried part of the open shell?
7. What is the composition of its shell?
8. How do fossil Lingulæ indicate the depth at which the inclosing sediment accumulated?

Crania (Fig. 102). *Ordovician to present.*

Shell small, nearly circular in outline, without a pedicle opening in the adult but cemented by apex or by entire surface of pedicle valve to the surface of a shell or other foreign object. Brachial (upper) valve conical, with beak almost central and directed posteriorly. In each valve there is a pair of widely separated muscle scars near the posterior margin and a pair close together near the center. Impressions of the pallial sinuses branch finger-like.

1. Sketch a valve, naming the valve and noting muscle scars if present.

SUBCLASS 2. ARTICULATA

Valves are held firmly together by teeth and sockets (whence the name from Latin *articulatus*, jointed). In living species the intestine is short and ends blindly, but in some Paleozoic forms it apparently opened through a foramen in the cardinal area of the brachial valve; if this opening was in life occupied by the anus, it suggests that a degeneration in structure has accompanied the retrogression in numbers for this subclass. Shell is calcareous.

The Articulata are divided into two orders. In the Protremata, the brachia are unsupported by a calcareous skeleton other than short crura (Platystrophia, Leptæna, Rafinesquina, Stropheodonta, Strophomena, Productus). The Telotremata are more advanced in the possession of the brachial support, the brachidium (Rhynchotrema, Terebratula, Atrypa, Spirifer).

Platystrophia (Fig. 103). *Ordovician and Silurian.*

Hinge line long. Both valves very convex, with a strong median fold in the brachial valve and a corresponding deep sinus in the pedicle valve. Entire surface covered with broad, strong, sharp plications (whence the name from Greek *platys*, wide, + *strophos*, a band). Shell impunctate but with a granulose surface.

This has developed from *Orthis lenticularis* of the Upper Cambrian, a plicate species with a smooth median fold upon the

pedicle valve and a smooth sinus upon the brachial. Later the median fold of the former becomes depressed between the two bounding plications forming the central plication of the median sinus of the adult shell, while the two plications bounding the early median sinus upon the brachial valve become, through their enlargement, two of the plications of the strong median fold of the adult. This shifting of the median sinus from brachial to pedicle valve may be due to the enlargement of the median lobe of the brachia, thus keeping the mantle from sagging at this point. All species of Platystrophia, whether from

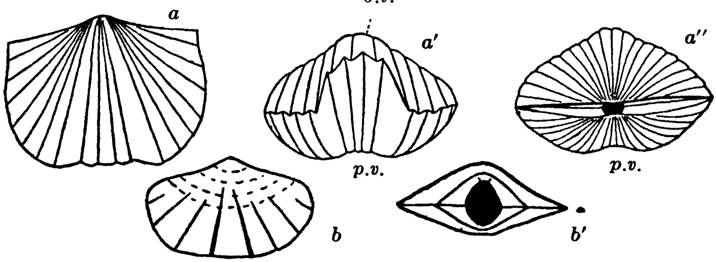


FIG. 103. — *Platystrophia lynx* (Eichwald), from the Upper Cincinnatian of Indiana. *a*, surface of pedicle valve, natural size; *a′*, junction of the two valves anteriorly; *a″*, junction of the valves posteriorly, showing the open delthyrium; *b*, exterior of pedicle valve of a very young individual, bhowing the introduction of plications; *b′*, posterior view of same; *b.v.*, srachial valve; *p.v.*, pedicle valve. The natural size of *b′* is noted by the black spot to the right. (From Cumings.)

the Ordovician or Silurian, pass through the same *Orthis lenticularis* stage (shown at the beak in well-preserved specimens). Platystrophia looks much like Spirifer, but has no calcareous supports for its brachia, and the cardinal area of the brachial valve is almost as high as that of the pedicle valve.

Platystrophia lynx is a very abundant species in the Middle and Upper Ordovician of North America.

1. Sketch (*a*) side view of entire shell, (*b*) view looking fully upon hinge line. Label in each the valves, cardinal areas, plications.
2. Describe as much of the evolution of Platystrophia, noted above, as is preserved upon the specimens at hand.

3. What can you say as to its probable ancestry?
4. What is the significance of the name?

Rafinesquina (Fig. 104, *A*, *B*). *Almost wholly Ordovician.*

Pedicle valve more or less convex, often without pedicle opening in the adult. The apex of its beak has a minute depression — the pedicle opening of the very young shell — but with age the pedicle usually disappeared, probably through resorption. The shell rested free upon the sea-bottom, but was held in place through social crowding, while the inner end of the pedicle opening became filled with lime, secreted probably by the extension of the ventral mantle. Brachial valve

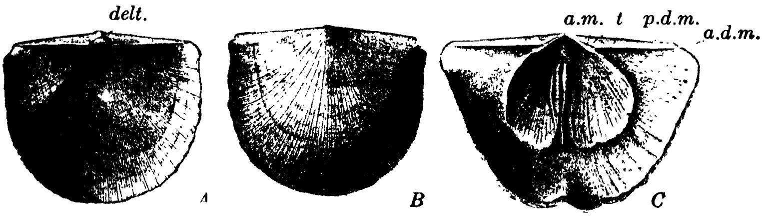


FIG. 104. — *A*, *B*, *Rafinesquina alternata* Conrad (× $\frac{3}{5}$), from the Ordovician of Cincinnati, Ohio. *A*, exterior of brachial valve. *B*, exterior of pedicle valve. *C*. — Strophomena, interior of pedicle valve. *a.m.*, adductor muscle scar; *p.d.m.*, posterior diductor muscle scar; *delt.*, deltidium; *a.d.m.*, anterior diductor muscle scar; *t*, tooth. (From Hall and Clarke.)

flat or concave. Hinge line straight. Surface with radiating striæ alternating in size. Shell punctate. (Name in honor of the French-American scientist, *Rafinesque.*)

R. alternata is the most widely spread and abundant species, being found almost everywhere in the Middle to Upper Ordovician of North America.

1. Sketch (*a*) exterior of pedicle valve, (*b*) cardinal areas of entire shell, (*c*) the cut portion of a vertical section through entire shell from beak forward. Label in all, where present, pedicle and brachial valves, hinge line, cardinal areas, beak, deltidium, front of shell.
2. Indicate in sketch 1 (*a*) the oldest portion of shell, stating your reasons.
3. How do you know that the convex valve is the pedicle valve?

4. Draw in your sketch of the pedicle valve the outline of the shell when half grown, stating how you know that this was its shape.
5. State whether the animal was attached or free when adult, giving reasons.

Leptæna (Fig. 105). *Ordovician to Mississippian.*

Pedicle valve convex, brachial concave. The flat portion of the shell is concentrically wrinkled; where these wrinkles cease the shell is abruptly deflected. Shell with closely ap-

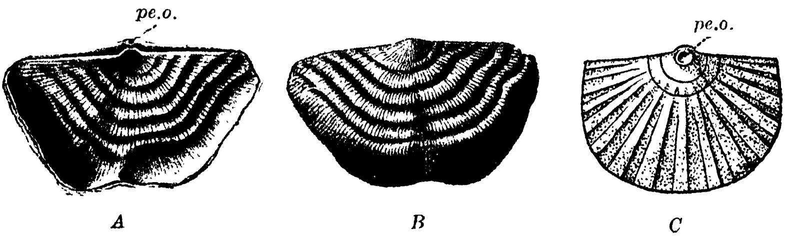


FIG. 105. — *Leptæna rhomboidalis* Wilckens. *A*, adult brachial valve (natural size), showing the exceptional retention of the pedicle opening (*pe.o.*) in the opposite (pedicle) valve. *B*, adult pedicle valve. *C*, pedicle valve (× 10), a young stage in the growth of the shell showing the beginning of the radiating striæ. *C* redrawn from Beecher. (*A* and *B* after Hall and Clarke.)

pressed valves, thin, *i.e.*, with very little space for the soft parts of the animal. Shell punctate.

1. Sketch (*a*) a view of exterior of pedicle valve showing the concentric wrinkles and the deflected anterior portion, (*b*) the cut portion of a vertical section through the entire shell from beak forward. Note pedicle and brachial valves.
2. How does Leptæna differ from Rafinesquina?

Stropheodonta (Fig. 106). *Silurian and Devonian.*

Shell similar to Rafinesquina but with the hinge margins marked by more or less long transverse ridges which terminate in teeth that articulate as teeth and sockets (whence the name from Greek *strophis*, a band, + *odous*, a tooth, a band of teeth). Shell punctate.

1. Sketch (*a*) exterior of pedicle valve, (*b*) cardinal areas of entire shell. Label valves, deltidium, transverse ridges.
2. How do you distinguish this genus from Rafinesquina?

Strophomena (Figs. 104, *C*, 107). *Ordovician.*

A *resupinate* Rafinesquina, *i.e.*, pedicle valve concave or sigmoid in section, and the brachial convex. The muscular area on the pedicle valve is sharply limited by elevated ridges. Shell punctate.

1. Sketch the cut portion of a vertical section through the entire shell from beak forward, labeling the pedicle and brachial valves.
2. How do you distinguish this genus from Rafinesquina?
3. Were the pedicle valve concave and the brachial convex in youth as in the adult state? Give reasons.

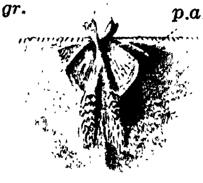


FIG. 106. — *Stropheodonta concava* Hall, from the Hamilton (Devonian) of New York (× ¾). Muscle area of the interior of a brachial valve. *p.a.m.*, the broad posterior adductor muscle scars; *c.p.*, cardinal process for attachment of diductor muscle; *gr.*, vertical grooving, or ridging, of the edge of shell at hinge line, giving rise to the name; *a.a.m.*, the elongate anterior adductor muscle scar. (From Hall and Clarke.)

Productus (Fig. 108). *Mississippian to Permian.*

Shell free, or anchored in the mud by the tubular spines growing from the convex pedicle valve. Brachial valve concave, spinose or lamellose. Hinge line not well developed, sometimes produced into ears. Entire surface marked with radiating ribs, or elongate pustules, which are usually studded with spines. Shell punctate. (Name from Latin *productus*, produced; so named from the prolongation of the beak of the pedicle valve beyond that of the brachial.)

Productus semireticulatus is world-wide in distribution, in the Mississippian and Pennsylvanian.

1. Looking fully upon the hinge line of entire shell, sketch a view showing brachial valve and umbo of pedicle valve; indicate valves, spines, radiating ribs.

2. State whether the animal was attached or free when adult, giving reasons.
3. How were the spines formed?
4. What caused the shell to be punctate? Are all brachiopod shells punctate?
5. What characteristic gives the genus its name?
6. Is *Productus semireticulatus* a good index fossil? Give reasons.

Rhynchotrema (Fig. 109). *Ordovician to Devonian.*

Valves thick, very convex. Pedicle valve strongly incurved at umbo, with thick concave deltidial plates. Entire surface covered with strong, radiating plications crossed by many concentric growth lines. (Name from Greek *rhynchos*, a beak, + *trema*, a hole; these forms usually have the beak of the pedicle valve perforated by a pedicle opening.)

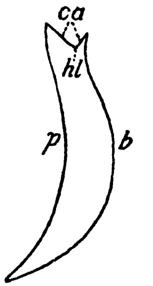


FIG. 107.—A diagrammatic longitudinal cross section of the brachiopod shell, *Strophomena planumbona* Hall (× 2). Section cut beside the deltidium. This is similar to Rafinesquina (Fig. 104), except that the convexity of the valves is reversed; *b*, brachial valve; *ca.*, cardinal areas of brachial and pedicle valves; *h.l.*, hinge line; *p*, pedicle valve.

R. capax was widely distributed throughout the shallow ocean covering much of North America during Upper Ordovician time. In some adults a large pedicle opening is present, in others it is absent.

1. Sketch (*a*) side view of entire shell, (*b*) anterior view, (*c*) cut portion of a vertical section through entire shell from beaks forward. Label valves, plications, growth lines, umbos.
2. Was this specimen attached or free when adult? Reasons.
3. By means of an ideal sketch, explain how the shell was built. What do the growth lines represent?
4. How do surface ornamentations, such as the strong plications of this genus, originate in the living animal? (See page 273.)
5. In sketch 1 (*c*) indicate by drawing in the muscles how the valves were opened and closed.
6. How do brachiopods eat? Breathe?
7. Do brachiopods live in the sea or in fresh waters?
8. At what depths do they live?

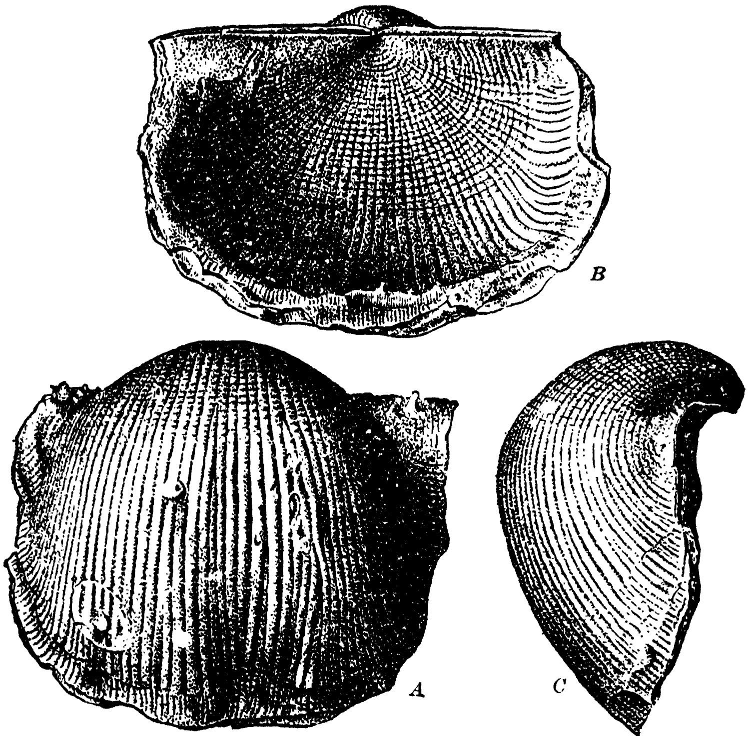


FIG. 108. — *Productus semireticulatus* Martin, from the Pennsylvanian of Indiana. Three views of one individual, natural size. *A*, pedicle valve; *B*, brachial valve with umbo of pedicle valve showing over edge of hinge line. *C*, side view. (After White.)

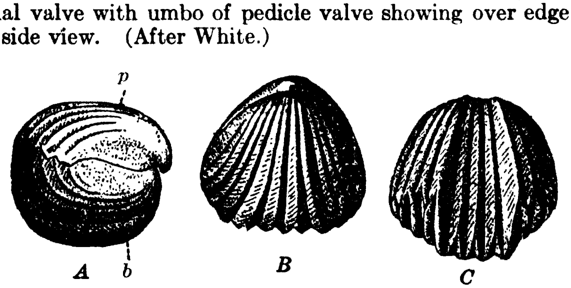


FIG. 109. — *Rhynchotrema capax* (Conrad), from the Upper Ordovician of Indiana. Natural size. *A*, side view of the joined valves; *b*, brachial valve; *p*, pedicle valve. *B*, brachial valve with beak of pedicle valve showing above. *C*, pedicle valve showing the deep median depression. (From Indiana Survey.)

Terebratula-like forms (Fig. 110). *Devonian to present.*

Shell usually biconvex, and elongate oval. Pedicle valve has generally a large circular pedicle opening (whence the name from the Latin diminutive of *terebratus*, perforated). Deltidial plates prominent. The old genus Terebratula has been subdivided into many genera.

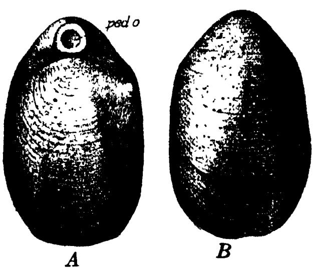


FIG. 110. — *Terebratula harlani* Morton from the Eocene of New Jersey. *A*, brachial valve, with pedicle opening (*ped.o.*) of opposite valve showing above. *B*, surface of pedicle valve (× ½). (After Whitfield.)

Rensselæria is an ancient type from the lower Devonian of North America and Europe. *Terebratula harlani* is a large form abundant in the Eocene of the Atlantic coast of North America. In the Upper Cretaceous of the same region is the coarsely punctate species *Terebratella plicata*. For *Terebratulina septentrionalis* see page 233.

Note the large pedicle opening, deltidial plates, and microscopic punctæ of *T. harlani*, the coarse punctæ of *T. plicata*.

1. What common name for brachiopods did Terebratula and allied forms suggest to early scientists?
2. Sketch side view. Label valves, pedicle opening.

Atrypa (Fig. 111). *Silurian and Devonian.*

Pedicle valve slightly convex, brachial usually very convex. Entire surface radially plicate, crossed by many more or less prominent concentric lamellæ of growth. Apices of spiral brachidia directed towards middle of brachial valve, hence the strong convexity of this valve.

Atrypa reticularis is very abundant throughout the world in the Silurian and Devonian. The Silurian forms are usually smaller with brachial valves much less convex and with less extensive lamellæ than the Devonian forms.

1. Sketch (*a*) exterior of pedicle valve, (*b*) exterior of brachial valve with umbo of pedicle valve showing, (*c*) interior of pedicle valve. Label

valves, plications, growth lines, impressions of pallial sinuses, adductor and diductor muscle impressions.

2. What function did the pallial sinuses perform?
3. How were the growth lamellæ formed? Illustrate by sketch.

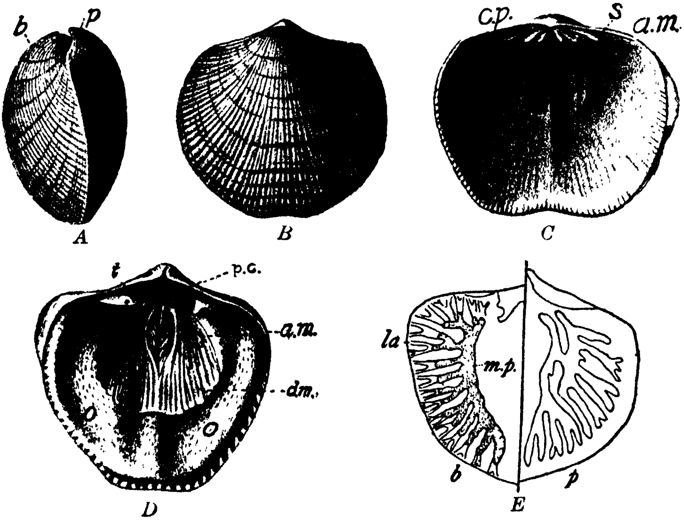


FIG. 111. — *Atrypa reticularis* Linne, from the Hamilton formation (Middle Devonian) of New York. Natural size. *A*, side view showing both valves. *B*, brachial valve. *C*, interior of brachial valve. *D*, interior of pedicle valve. *E*, mantle of the living *Terebratulina coreanica*. The one valve is drawn with the sinuses (spaces in the mantle cavity) filled with eggs. The eggs have not been indicated in the mantle of the pedicle valve. Beneath these sinuses roughened thickenings of the shell frequently occur, especially in the old shells as at *o* of figure *D*. *a.m.*, adductor muscle scar (in figure *C* it includes all the scars within the shell); *b*, brachial valve; *c.p.*, cardinal process; *d.m.*, diductor muscle scar; *la.*, lacuna; *m.p.*, main pallial sinus; *o*, ovarian markings on shell; *p*, pedicle valve; *p.c.*, cavity for attachment of pedicle; *s*, socket; *t*, tooth. (*A* to *D* after Hall and Clarke; *E* after Morse.)

Spirifer (Figs. 100, 112). *Silurian to Permian.*

Shell usually wider than long, with straight hinge line. Pedicle valve usually with high cardinal area and strong median sinus. Brachial valve with very low cardinal area and strong median fold. Surface of entire shell radially plicate or striate,

or with the fold and sinus not plicate, crossed by more or less strong growth lines. Brachidia are spirals (whence the name, from Latin *spira*, a spire, + *ferre*, to bear); the spirals are directed towards the cardinal angles (hence the great width of the shell); some Spirifers have spirals of 35 revolutions. The animal was anchored by a short pedicle which passed out through the delthyrium. The old genus Spirifer of authors has been subdivided into many new genera and subgenera made necessary by the variations in the vast number of species found.

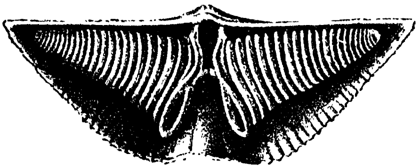


FIG. 112. — *Spirifer mucronatus* Conrad, from the Hamilton (mid-Devonian) of New York, showing the long, tapering spirals attached to the inside of the brachial valve for the support of the brachia. Natural size. (After Hall and Clarke.)

S. mucronatus is a characteristic Middle to Upper Devonian species of North America; *S. disjunctus*, an Upper Devonian species throughout North America and most of the world; *S. cameratus*, a widely distributed North American Pennsylvanian species.

1. Sketch (*a*) side view of entire shell, (*b*) exterior of pedicle valve, (*c*) view looking directly upon the hinge line, (*d*) interior of brachial valve showing the spirals. Indicate in sketches the valves, plications, growth lines, median sinus, median fold, hinge line, cardinal areas, delthyrium, spirals.
2. What is the relation of the mantle to the shell?
3. What was the function of the spirals?
4. How do you distinguish this genus externally from Platystrophia?
5. What is the significance of the name Spirifer?
6. What is the geologic range of the class Brachiopoda?
7. During what periods did the greatest number of brachiopods live?
8. How many species are living at present?

EVOLUTION OF THE MOLLUSCOIDEA

Both Bryozoa and Brachiopoda have probably descended from some group of worm-like ancestors in the pre-Cambrian. The ciliated larvæ suggest a relationship to the Trochelminthes. In their subsequent evolution both classes developed a lophophore,

a similar manner of obtaining food, a dorsal nerve ganglion, an external skeleton, and nearly always a U-shaped digestive tract.

The two classes diverged especially in size. The Bryozoa remained minute but this handicap was overcome by their colonial habit; they formed solid or branching masses attached to some solid object at the bottom of the water. The brachiopods became comparatively large and could thus meet their environment as individuals, without the necessity of becoming colonial. Brachiopods very early branched into two distinct lines. The more primitive groups (subclass Inarticulata) retained throughout life the horny shell characteristic of all brachiopods during late larval life. The valves were opened and closed by a sliding movement worked by several pairs of muscles. The remaining groups (subclass Articulata) secreted a shell predominantly of lime carbonate succeeding the larval horny shell, and this continued throughout life. Upon this harder shell they developed teeth and sockets for the articulation of the valves, in place of the more cumbersome arrangement characteristic of the Inarticulata.

Molluscoidea as Rock-Builders

Because of their branching habit, many bryozoöns acted like corals of similar habit and were the binding agents in the construction of reefs. Their colonies not only gave harborage to other forms of life, but tended to hold drifting sediment. Bryozoöns, aided by brachiopods, corals, echinoderms, and algæ, were most important as rock-builders during the Paleozoic. The Ordovician bryozoa-brachiopod reef masses from the Cincinnati region are notable. The Permian (Zechstein) Fenestelloid reefs of Thuringia, Germany, reach at times a thickness of 300 feet; they are now structureless dolomite and, being more resistant than the stratified deposits surrounding them, they stand up as steep, block-like hills; these are often surmounted by castles. Bryozoa became less important as rock-builders during the Mesozoic and Cenozoic, but Membranipora reefs up to 100 feet in height are found in the Pliocene of the Peninsula

of Kerch, between the Black Sea and the Sea of Azof. Not infrequently brachiopods occur to the exclusion of all other forms, giving rise to a pure brachiopod coquina (Fig. 113). Such are the Platystrophia coquina and the *Dalmanella testudinaria* coquina of the Ordovician of the southern Appalachian Region, the Silurian Pentamerus coquina of Europe and America. Brachiopods



FIG. 113.— An Ordovician coquina from the southern Appalachian region. These unbroken shells show that they accumulated some distance from shore.

became less important as rock-builders during the Mesozoic and of very slight value during the Cenozoic.

1. Divide the phylum into classes and all minor subdivisions, giving an example of each.
2. Which class has the best-known fossil representatives?
3. What do Bryozoa and Brachiopoda possess in common that they should be placed in the same phylum?
4. Do these two classes enter into direct competition as regards food-getting?
5. How do the Molluscoidea differ from the Cœlenterata in the following characters: (*a*) habitat, (*b*) protecting and supporting skeleton, (*c*) locomotion, (*d*) food, (*e*) its capture, (*f*) its intake, (*g*) digestion, (*h*) blood circulation, (*i*) excretion of waste, (*j*) respiration, (*k*) nervous system, (*l*) sense organs, (*m*) reproduction, (*n*) geologic range? How do the Molluscoidea differ from the Annelida in these characters?
6. Outline briefly the evolution of the Molluscoidea.
7. Discuss the importance of Molluscoidea as rock-builders.

CHAPTER XII

PHYLUM XI. MOLLUSCA (MOLLUSKS)

The Mollusca as a group possess bilaterally symmetrical, unsegmented bodies enveloped in a sac-like fold, the mantle, which secretes a protective exoskeleton, the shell. The primitive bilateral symmetry is often obscured by a secondary torsion of the body.

They are mostly free-living, able to crawl, swim, and burrow.

The general external divisions of the body are the head (absent in the Pelecypoda), possessing mouth, various kinds of appendages, and nearly all the organs of special sense; the foot, a ventral projection of various shapes; and a dorsal portion, including the viscera and covered by the mantle which secretes a shell.

The digestive system consists of three divisions: (*a*) an anterior division, consisting of the mouth, buccal cavity (absent in most pelecypods), and œsophagus; the buccal cavity contains the characteristic radula; (*b*) a middle division, the stomach, into which pours the secretion of the liver, an important digestive gland; (*c*) a posterior division, the intestine, ending in an anus.

The circulatory system consists largely of closed tubes, although there are some open sinuses. It includes a heart consisting of one ventricle and usually two auricles (in Nautilus, four).

The blood is a fluid with both nutritive and respiratory function. It varies in color among different mollusks, being colorless, bluish from the presence of hæmocyanin, or red from the presence of hemoglobin.

Respiration is usually effected by ctenidia or gills — specialized expansions of the ventral surface of the mantle, through

which passes nearly all of the blood just before entering the auricles on its way back from circulation throughout the body.

The excretory system consists primarily of renal sacs or kidneys — tubes which in most mollusks connect the body cavity with the exterior through the mantle cavity. Nearly all of the venous blood traverses the kidneys on its way to the gills and is by them purified of the nitrogenous waste products of metabolism.

The nervous system consists essentially of a nerve ring surrounding the œsophagus, giving off four nerve cords, a pair to the dorsal region of the body and a pair to the ventral region.

The sexes are usually separate. The union of spermatozoa and ova is followed by laying of eggs, usually in a gelatinous or leathery matrix.

Most mollusks (Cephalopoda excepted) in their development pass through a larval stage, the veliger, in which the tiny, free-swimming form possesses a thickened retractile rim in front of the mouth, which bears a circlet of cilia and is called the velum. A shell gland on the dorsal surface secretes the shell which is characteristic of most Mollusca. There are over 60,000 living species of mollusks.

Derivation of name. — Latin *molluscum*, a soft-bodied animal.

The Mollusca are divided into the following classes; the names are mainly references to the form assumed by the foot:

CLASS A. AMPHINEURA (CHITONS)

The Amphineura are distinguished by the bilaterally symmetrical body, with mouth and anus at opposite ends. They possess a foot adapted for creeping. The mantle surrounds

the body either entirely (in the worm-like Aplacophora) or only dorsally (in the true chitons, the Polyplacophora), and secretes in the former order calcareous spicules, in the latter a dorsal armor of eight plates.

The Aplacophora are by some classified with the primitive Archiannelida of the annelid worms. The chitons (Polyplacophora) are marine, occurring in all oceans, generally in shallow water. They live on or under stones, where they feed, largely upon algæ. Amphineura have existed since Ordovician times. All fossil forms are members of the Polyplacophora, — those possessing a dorsal armor (Fig. 114).

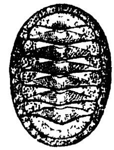


FIG. 114. Dorsal view of a living chiton (*Chætopleura apiculata* Carpenter) from Massachusetts (but abundant from Cape Cod to Florida). (From Verrill and Smith.)

CLASS B. PELECYPODA (LAMELLIBRANCHIA)

Type of class, *Venus mercenaria* (Figs. 115–118).

Venus mercenaria, called variously the hard or little-neck clam or quahog, is a warm water form with range of greatest abundance along the southern Atlantic coast from the southern side of Cape Cod to Texas. North of Cape Cod it occasionally occurs up to the Gulf of St. Lawrence. It is found most abundantly on sandy and muddy flats just below low-water mark, but its possible range is great, from high tide line to a depth of over 50 feet. It burrows into the mud to a depth just sufficient to cover the shell. This species has inhabited the Atlantic coast since Miocene time.

The **soft body** (Fig. 115, *B*) is inclosed in a calcareous shell which consists of two halves, the *valves*, joined by a hinge along the dorsal edge. From one end of the ventral or open edge of the shell protrudes a muscular, tongue-like body, the *foot,* by means of which the animal may slowly make its way through the sand or mud, in which it lies superficially buried. The presence of the foot indicates that end to be anterior and it is in that direction that the animal moves. From the opposite, the posterior end of

the shell, project two tubes, the *siphons*, united almost to their ends.

When the valves are opened, each is found to be lined by a thin membrane, the *mantle.*

The two lobes of the mantle are attached to the body dorsally, and extending down over the sides, come closely to-

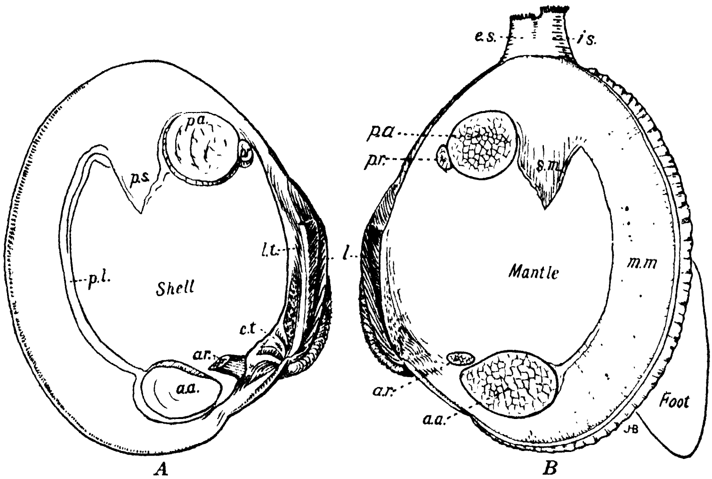


FIG. 115. — The quahog, *Venus mercenaria* Linné, in position of feeding. (× $\frac{2}{3}$.) Left valve separated from its mantle and muscles which are left lying in the right valve. *a.a.*, anterior adductor muscle and scar; *a.r.*, anterior retractor muscle (a portion of it is attached to the left valve); *c.t.*, cardinal teeth; *e.s.*, excurrent siphon; *i.s.*, incurrent siphon; *l*, ligament; *l.t.*, lateral teeth; *m.m.*, mantle muscle; *p.a.*, posterior adductor muscle and scar; *p.l.*, pallial line (the scar left by the mantle muscle); *p.r.*, posterior retractor muscle and scar; *p.s.*, pallial sinus (the scar left by the siphonal muscle); *s.m.*, siphonal muscle.

gether along the ventral edge, thus inclosing the body of the animal as in a sac. The siphons are merely projections of the mantle edge united into muscular tubes. The lower is the incurrent or branchial siphon; it draws in water carrying food to the mouth and oxygen to the gills. The upper is the excurrent or anal siphon; it discharges the waste products of the digestive system and the water which has passed

over the gills and has hence become impure with the products of respiration.

The organs of **respiration** are the gills and mantle. The *gills* are two thin, curtain-like folds hanging free on each side of the main body mass just beneath the mantle (Fig. 116, *B*). Each

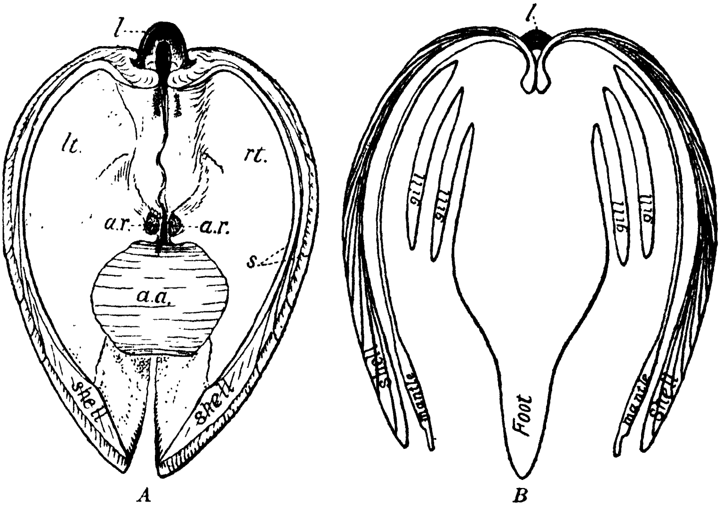


FIG. 116. — Vertical section through the quahog, *Venus mercenaria* Linné. *A*, looking into the shell toward the anterior end. *a.a.*, anterior adductor muscle; *a.r.*, anterior retractor muscle scar; *l*, ligament, showing its C-spring shape; *lt.*, left valve; *rt.*, right valve; *s*, section of shell showing the increments of growth. *B*, an ideal section through a pelecypod. Such a section may be compared to a book, with binding along the dorsal (ligamental) edge and with the valves corresponding to the covers, the mantle lobes to the fly leaves, the two pairs of gills to the first two and the last two pages and the foot to the remainder of the leaves fastened together.

of these four gills is double, being a very narrow bag open dorsally. From the union of these gills with each other and with the mantle on each side, and antero-dorsally with the viscero-pedal mass (the main body mass into which the foot merges), it results that the gills form a partition extending through the mantle cavity, dividing it thus into two chambers. Of these the

upper is called the cloacal and from it passes the exhalant or anal siphon; the lower is called the branchial and into it opens the inhalant or branchial siphon (Fig. 115).

The gills are vertically striated. Microscopic examination shows these striæ to be parallel hollow tubes. Thus it is seen that each lamellar half of a gill is composed of a series of these tubes placed side by side and bound together. Through them the blood circulates and their walls are bathed on all sides by the water which pours into the gills between the tubes. As these walls consist of a single layer of cells, there is a ready interchange between them of the waste gases (which the blood brings from the body to the gills) and the oxygen of the water.

Water, admitted through the branchial siphon into the branchial chamber of the mantle cavity, is driven in a rapid continuous current into the gills by the cilia bordering them. From the gills the water passes in a strong current into the cloacal chamber and thence through the exhalant siphon to the exterior. The mantle likewise functions in respiration, being a thin-walled reservoir for blood in contact with the water.

Food as well as oxygen is brought to the animal in the water introduced by the branchial siphon into the mantle cavity. The principal food is diatoms, though according to the location and the season the clam feeds also on small crustaceans and rotifers, protozoöns and larvæ of mollusks. These small food particles are swept in with the current and become entangled in the mucus poured out by the gland cells of the gills. Movements of the cilia on the gills urge these food masses on to the *mouth.* This lies in the median line just below the anterior adductor muscle. Triangular flaps, the labial palps, unite above and below it to form an upper and a lower lip. The food is swept by the cilia on these palps into the mouth and thence passes through the œsophagus into the *stomach.* Digestion is accomplished chiefly through the agency of the fluid poured into the stomach by the liver, a paired dark brown mass surrounding the stomach. The intestine leads from the stomach as a narrow tube which makes several convolutions in the visceral

mass, and passing backward, opens into the exhalant siphon just over the posterior adductor muscle.

The chief organ of the **circulatory system** is the *heart*, situated saddle-like upon the intestine, dorsally near the hinge. It consists of one ventricle and two auricles, and is inclosed in a

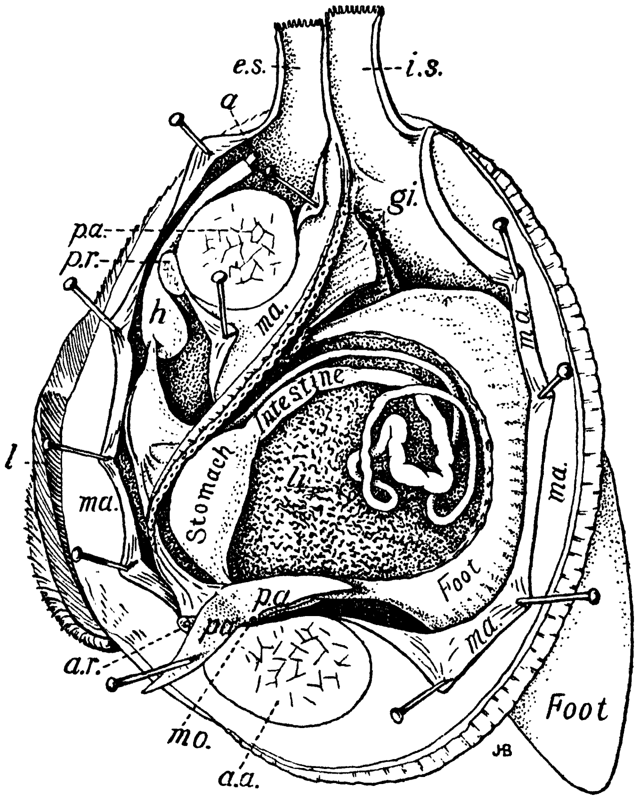


FIG. 117. — The quahog, *Venus mercenaria* Linné, in position for feeding (natural size), partly dissected lying in the right valve. *a*, anus; *a.a.*, anterior adductor muscle; *a.r.*, anterior retractor muscle; *e.s.*, excurrent siphon; *gi.*, cut edges of gills; *h*, heart; *i.s.*, incurrent siphon; *l*, ligament; *li.*, liver; *ma.*, mantle cut and pinned back to show the organs within its cavity; *mo.*, mouth; *pa.*, palps or lips at side of mouth; *p.a.*, posterior adductor muscle; *p.r.*, posterior retractor muscle.

membranous chamber, the pericardium. (This is the only body cœlome possessed by the pelecypod.) The blood is a colorless liquid and forms an important part of the mass of the body. It is pumped by the ventricle into two aortæ, the anterior and the posterior, which branch into arteries and open sinuses, thus penetrating all parts of the body with its load of food and oxygen. From these sinuses the blood is gathered up by veins and returned to the auricles, the larger part passing through the gills on its return.

The **excretory organs** are the nephridia, a pair of dark, U-shaped tubes, of which one arm is glandular and spongy, the kidney, and the other is non-glandular and thin-walled, the bladder. They are situated in the postero-dorsal region. The kidney communicates with the pericardium and the bladder opens into the mantle cavity. Waste material gathered from the body by the blood is extracted from the blood by the kidneys and passed out of the body into the mantle cavity by the exterior opening of the bladder.

The **nervous system** consists of three pairs of large ganglia and their connectives: a ganglion on each side of the œsophagus, united by a nerve cord and connected by other nerve cords with the two pedal ganglia in the base of the foot, and the two visceral ganglia near the posterior adductor muscle.

Sense organs. — All of the soft parts are sensitive to touch, but this sense is especially well developed on the edges of the mantle and of the siphons. There are no definite eyes, but there are pigmented areas in the siphonal region, which are sensitive to light, but which can distinguish no color or form. The *osphradium* is a small organ at the point of attachment of the gills whose function is supposed, from its situation, to be to test the water as it flows into the gills. It has been suggested that it may possess the undifferentiated chemical sense of smell and taste combined. The *otocysts* are spherical cavities filled with liquid in which is suspended a solid particle, the otolith. These are balancing organs, serving to keep the clam upright. They are supposed likewise to have an auditory function since

pelecypods are able to sense sounds transmitted through the water.

The following are some of the principal **muscles** of the body (Figs. 115, 116):

1. *Mantle muscle.* This extends around the edge of the mantle lobe and unites it to the shell. The mark left on the shell by this attached mantle edge is called the *pallial line.*

2. *Siphonal.* This is a specialized part of the mantle muscle, originating from the siphons and serving to draw them into the shell. It spreads out fan-wise in proportion to the length of the siphons, and its insertion on the valve interrupts the evenly curved line of attachment of the mantle muscle. Hence the pallial line is indented by the *pallial sinus.*

3. *Adductor.* These are two large cylindrical muscles which pass transversely across the body and are attached at each end to one of the valves; their insertion leaves on each valve an anterior and a posterior muscle impression. The contraction of these muscles pulls the valves together and closes the shell: a chitinous *ligament,* tough and elastic, unites the valves externally. This, like a C-spring, exerts a constant tendency to straighten and thus to cause the valves to open to a certain extent. Beyond that distance it tends to prevent the valves from opening. When the adductor muscles, therefore, relax, the valves yield to the action of the ligament and open.

4. *Foot muscles.* The foot is drawn into the shell by the anterior and posterior retractor muscles and is extruded by a single protractor muscle which spreads fan-like over the whole visceral mass and by the compression of which the foot is forced out. The attachment of these muscles is marked by three faint scars on each valve — that of the anterior retractor and the protractor near the anterior adductor impression, and that of the posterior retractor just dorsal to the posterior adductor. The foot itself is likewise very muscular.

That part of the mantle which is outside the pallial line is free, is somewhat thickened, and contains the more active **shell-building glands.** The series of glands around the edge of the

mantle secretes a dark horny layer (conchiolin); the glands immediately back of these secrete a much thicker calcareous layer. These materials are probably derived from the blood by the epithelial cells of the mantle. They are deposited in a liquid state but harden immediately upon deposition. The conchiolin is not easily affected by acids and thus protects the calcareous layers beneath. Thus the shell grows by the continual building out of its edge through successive depositions of lime and of conchiolin. In this way are formed the two outer of the three layers of which the shell consists.

After the glands around the edge of the mantle have secreted these layers in the manner described, other glands covering the whole external surface of the mantle line the shell thus formed with the inner pearly layer.

A transverse section through a valve reveals (1) an outer horn-like layer of conchiolin secreted only by the extreme edge of the mantle and hence always projecting slightly in advance of the other layers; (2) a middle prismatic layer composed of calcareous prisms placed at right angles to the shell surface, and separated by layers of conchiolin; and (3) an inner pearly layer, composed of thin alternate layers of calcareous matter and of conchiolin, parallel to the shell surface. This presence of conchiolin throughout the shell furnishes it with a sort of membranous framework sufficient in amount to enable the shell to retain its shape after the removal by acids of all calcareous matter.

When the seasons, temperature, or food supply are unfavorable to rapid growth, the mantle does not increase in size. The glands which secrete the shelly matter continue active, however, and their deposit forms an extra thickness on the shell already formed, especially around its edge. With the return of conditions favorable to the growth of the animal, the mantle grows forward, again extending the shell and leaving behind as a thickened line the deposit of shelly material formed during the quiescent stage. The shell thus bears a succession of raised *lines of growth* or varices (Fig. 118), indicating inactive periods and separated by thinner bands marking periods of active expanding growth of the mantle. There may be many

such growth lines in a year, as favorable and unfavorable conditions alternate, minor oscillations in conditions as that between high and low tide, day and night, etc., being indicated by very fine growth lines.

The dorsal or cardinal margin of each valve is strengthened by a thick vertical plate, the *hinge plate.* Upon this are strong projections and ridges forming a system of *teeth* and *sockets*, the teeth of one valve fitting into the sockets of the other. This interlocking apparatus constitutes the *hinge* of the shell; by means of this an exact closure of the valves necessarily occurs. The teeth are of two kinds, the anterior or cardinal, consisting of short transverse elevations, and the posterior or lateral, longer teeth parallel with the dorsal margin of the valve.

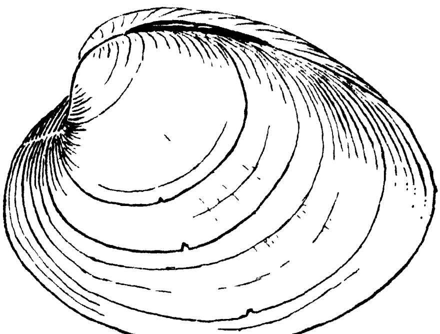


FIG. 118. — The quahog, *Venus mercenaria* Linné, showing how age may be reckoned by counting the more prominent growth lines. Three and a half years old; three inches long. At the same time each year a notch was filed into the edge of the shell. (Redrawn from Belding.)

The rounded, elevated portion of each valve is called the *umbo;* it ends in a point, the *beak*, which curves toward the anterior end of the shell. This is the oldest portion of the shell and from it growth has proceeded. Hence the beak is the initial point of the concentric growth lines. Under the beak and anterior to it is a depression called the *lunule.*

The **sexes** are distinct. The reproductive elements are extruded into the mantle chamber and out into the surrounding water through the exhalant siphon. Millions of eggs and spermatozoa are produced, most of which perish, since it is only by chance that their union is effected and fertilization thus results.

Development starts directly in the fertilized egg; this results in the formation of a blastula which soon invaginates, thus passing into the gastrula stage. Thus, about ten hours after the egg has been fertilized, the embryo has become a spherical gastrula $\frac{8}{100}$ of a millimeter in diameter. Up to this time it has remained inclosed in the gelatinous case which covered the egg, but in its gastrula form it is provided with hair-like cilia which start it rapidly revolving, and soon it breaks through the transparent egg case and escapes as a trochosphere larva into the water. This *trochosphere* (trochophore) stage is characterized by a top-shaped body with cilia confined to the blunt anterior end, by a primitive mouth, and by the appearance of a shell gland opposite the mouth.

During the next twenty-four hours a tiny valve, secreted by the shell gland, forms on each side of the animal and slowly increases in size until it completely envelops the embryo. The dorsal portion alone remains uncalcified, and by additions of conchiolin it develops into the C-spring ligament. Other changes taking place along with the formation of this shell are the development of a velum, a peculiar kind of extensible ciliated swimming organ, the development of a foot, and the increasing complication of the digestive tract. This shelled swimming form, succeeding the shell-less swimming trochosphere, is called the *veliger*. All these changes, from gastrula to veliger, are accompanied by but small increase in size; but at the end of the veliger period, which endures from six to twelve days, according to the temperature of the water, important changes are inaugurated which lead rapidly toward the attainment of the adult form. The animal increases in size, and with the complete disappearance of the velum and the loss of the swimming function of the foot, it leaves the free swimming life and sinks to the bottom.

A gland in the foot secretes the *byssus*, fine, tough threads by which the animal becomes attached to sand grains, shells, eel-grass, or other objects. It is, however, an active animal at this stage and constantly travels from one place of attachment

to another, breaking its byssal threads and forming new ones. The addition to the shell from this time on is coarser, whiter, and characterized by well-marked concentric growth lines. A sharp line separates this new shell growth from the earlier larval shell, the *prodissoconch*, which had a smooth, homogeneous structure (compare Fig. 127, *pd.*).

During this attached stage the various organs of the body slowly take on adult characteristics. The clam remains attached until it has become large enough to make its way into the sand. When it is about 9 mm. long the byssus disappears and the active foot burrows into the sand, pulling the shell after it in a series of jerks, the siphonal end of the animal being left projecting upward in the burrow. Hereafter it moves but little, occasionally, however, crawling short distances.

Though the young clams sustain heavy losses before they become able to burrow, the adult animal is one of the hardiest of pelecypods. It is very insensible to temperature changes and to changes in the saltness of the surrounding water, and it can endure long exposure to the air. There are few natural enemies of the adult clam. Even the starfish and oyster drill are not very destructive.

They are known to live four or five years and perhaps in some cases longer. Growth is most active in August, being nearly at a standstill from November 1 to May 1. One individual with length of an inch when measured was found to have grown $\frac{7}{8}$ of an inch the following year. Fertilization (in New England) occurs from early June to the middle of August.

1. What is the common name of *Venus mercenaria?*
2. Its present range of habitat? Its geologic range?
3. Examine the specimens preserved in alcohol: (*a*) with valves held apart exhibiting relation of mantle to shell, the gills, muscles, and foot; (*b*) with one valve raised preserving attachment at hinge, showing upon the mantle the following muscles and upon the shell their attachment scars: (1) mantle, (2) siphonal, (3) adductor, and (4) foot.
4. Examine a dried specimen, sectioned through the two valves from ligament anteriorly, showing the ligament which opens the valves, one of the muscles which close it, the lines marking the growth of each

valve in length and thickness. (The specimen should first be sectioned, then all the soft parts removed except the muscles, soaked in corrosive sublimate for a day or two, and thoroughly washed and dried.)

5. What is the mantle? Its function? What mark does it leave upon the shell?

6. What are the siphons? Their functions? What mark does their presence make upon the shell and why?

7. Compare a transverse section of this pelecypod to a book.

8. Explain in detail how respiration is effected.

9. What does the clam eat? Explain the process of getting the food, its digestion and assimilation.

10. Describe briefly the blood circulatory system.

11. How are the different waste products of the body thrown off?

12. Of what does the nervous system consist?

13. What sense organs does the clam possess? Their function?

14. Name four sets of muscles, explaining the function of each.

15. Describe in detail the growth of the shell.

16. What is the origin of pearls?

17. Sketch the exterior of a valve, noting the umbo, beak, growth lines, lunule.

18. Why are the growth lines arranged concentrically?

19. Explain the occurrence of the few strong growth lines upon the shell.

20. How can the mantle secrete three layers of shell?

21. Sketch interior of a valve, locating hinge margin, ligament, hinge plate, teeth (cardinal and lateral), pallial line, pallial sinus, the two adductor and three foot muscles.

22. What is the function of the teeth?

23. How is the foot protruded?

24. What is the relation of the pallial sinus to the siphons?

25. How are the valves opened? How closed? Illustrate with sketches.

26. How do you distinguish the right from the left valve?

27. Are the two sexes united in one individual?

28. Describe the development of the clam from the union of spermatozoön and ovum to its adult state.

General Survey of Class Pelecypoda

Pelecypods are compressed, usually symmetrical, mollusks protected by a calcareous shell of two, usually equal, valves and possessing a ventral, often hatchet-shaped, foot capable of burrowing in sand.

There is no distinct head, nearly the whole ventral aspect of the animal consisting of the muscular mass of the foot.

The presence of a siphon in the various species of pelecypods is nearly always indicated on the valve by a pallial sinus (see page 267), though in a few exceptional species there is no such indication of its presence. When no pallial sinus is present, the pallial line is called simple. The portion of the mantle which is outside of the pallial line bears the pigment glands and in certain pelecypods papillæ and tentacular processes. On this edge likewise are the visual organs when such are present, as in Pecten.

Pearls are calcareous concretions of peculiar luster formed as a product of abnormal secretion of the mantle, probably always in response to some irritant. "True" spherical pearls are due to the presence in the inner layer of the mantle of a closed sac of the shell-secreting epithelium — a sac which is not continuous with the secreting surface of the epidermis which lays down the shell. They are apparently formed in response to some irritant which brings into the deeper tissues of the mantle the pearl-forming cells which normally are on the outside of the mantle and which secrete the mother-of-pearl lining of the shell (see also page 268). "Blister" pearls are formed of protective nacreous matter deposited by the mollusk around the point of invasion of a boring parasite, such as minute species of worms. The Chinese and Japanese have taken advantage of this disposition of the mollusk to form pearly protective layers around offending objects. Pearl culture has been carried on in the East for many centuries. Genuine "natural" precious pearls are produced by varieties of the genus Meleagrina, represented in tropical regions all over the world.

All surface irregularities of the shell, such as lines, knobs, spines, etc., are simply the result of corresponding modifications of the margin of the mantle. Thus spines indicate the existence of finger-like projections extending out from the edge of the mantle and secreting around themselves these hollow shelly processes. Ribs on the shell indicate wavy undulations of the

mantle margin. The hinge teeth are probably derived from the crenulations or ribbing of the surface of the shell.

The digestive canal is much coiled, consisting of mouth, œsophagus, stomach (into which open two large digestive glands), and intestine, ending in an anus. The blood of pelecypods contains nucleated amœboid corpuscles and in some forms, such as *Arca pexata*, the bloody clam, some species of Tellina, etc., there are also present non-amœboid corpuscles containing hemoglobin; in such cases the blood is red. In other forms (some Veneridæ, Cardiidæ, etc.) the blood is bluish, owing to the presence of hæmocyanin. In Venus, Ostrea, Pecten, etc., it is nearly colorless.

The nervous system consists typically of four pairs of ganglia, cerebral, pleural, pedal, and visceral, united by nerve connectives. The usual sense organs are otocysts and osphradia. Eyes are at times present on the mantle edge; these range from simple pigmented cells to the complicated eye of Pecten.

The sexes are usually separate. The order Anatinacea is hermaphroditic, as also the Cyrenidæ and certain other isolated genera and certain species of Pecten, Ostrea, Anodonta, etc.

The valves are held together by one or two strong adductor muscles, passing transversely from valve to valve, and their opening is effected, upon relaxation of this muscular tension, by external or internal *ligaments*. The external ligament, acting on the principle of a C-spring, is exemplified in Venus (Fig. 116, *A*). The internal ligament (*resilium*) functions as would a piece of elastic rubber between a door and its jamb. Its triangular shape (narrower at the hinge than internally) keeps the hinge portion of the valves firm while causing the opposite side to open. It may be single, as in Mactra and Ostrea (Fig. 122, *l*), or multiple, lying in a series of pits, as in Inoceramus. In some forms, such as Mactra, a special spoon-shaped projection from the hinge, the resilifer, or ligament pit, lodges the internal ligament. The ligament, whether external or internal, is, in its origin, continuous with the shell, being the part of the original embryonic shell which remained uncalcified.

The dorsal hinge of interlocking teeth brings about an exact closure of the valves so that even at the approach of danger, when the valves are hastily closed, they will meet edge to edge and thus prevent the access of any enemy to the soft and tempting body portion.

The two valves are usually similar in size and appearance, one being the " mirror image " of the other. They are distinguished as the right and the left valve, that to the right and left respectively, as the shell is held with beaks uppermost and with the anterior extremity directed outward.

The following are the criteria for distinguishing the anterior and posterior ends of a valve.

1. The umbos are nearly always directed forwards.
2. The pallial sinus is posterior.
3. The external ligament is never entirely anterior, and is usually mostly posterior to the beaks.
4. When there is but one adductor impression it is the posterior.

Both pelecypods and brachiopods have an external, bivalved, calcareous shell. That of the former differs from that of the latter as follows:

1. Valves are right and left, not dorsal and ventral.
2. Valves are usually inequilateral and equivalved.
3. Umbos are never perforated by a pedicle opening.
4. Teeth when evident are present in both valves.
5. Ligament is present.

Shell accessories are present in some genera, such are described under Teredo.

The anterior adductor muscle may become diminished in importance or entirely absent. In such a case the posterior adductor necessarily assumes a more central position as a result of the greater demand placed on it for mechanical efficiency. The disappearance of the anterior adductor and the assumption by the posterior of a more central position are accompanied by a shortening of the antero-posterior axis of the shell and a proportional lengthening of the dorso-ventral axis. Such a transformation has been effected in the oyster (Fig. 122).

Pelecypods range from the lower Paleozoic to the present time, being, however, extremely rare in the Cambrian. In the Upper Cambrian they are represented by such genera as Glyptarca. Their presence in the Lower Cambrian is doubtful; such forms as Fordilla (oval and concentrically striated) are probably phyllopods, like Estheria, or ostracods.

Derivation of name. — Greek *pelekus*, an ax, + *pous* (*pod*), foot. The foot of many pelecypods is shaped like an ancient battle-ax.

Nucula (Fig. 119). *Silurian to present.*

Valves small, oval or triangular, with a pearly interior. Hinge line *taxodont*, *i.e.*, bearing a series of small, nearly equal, transverse teeth. Beak exceptional in facing the posterior end of the shell, *i.e.*, the beak faces away from the mouth, which is near the anterior edge of the shell. Mantle lobes free, without siphons, hence pallial line simple. Two adductor muscles present. Name from Latin *nucula*, a little nut.

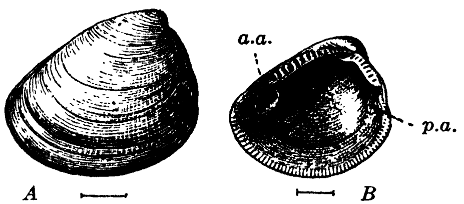


FIG. 119. — *Nucula proxima* Say, from the Miocene of Maryland. Natural size. *A*, exterior of left valve. *B*, interior of right valve showing the two muscle scars and the numerous teeth in a row (taxodont dentition). *a.a.*, anterior adductor muscle scar; *p.a.*, posterior adductor muscle scar. (From Glenn.)

Especially abundant in the Hamilton, Pennsylvanian, and Cretaceous of North America, but widely represented by both fossil and recent forms in Europe and Asia as well.

1. How do the beaks of Nucula differ from those of most other pelecypods? How is this known?
2. Sketch an interior view of one valve, indicating anterior and posterior ends, beak, hinge line, teeth, muscle scars, pallial line.
3. What is the function of the teeth?
4. Mention three characters which determine this to be a pelecypod shell rather than a brachiopod.
5. What is the probable origin of teeth in pelecypods?

Inoceramus (Fig. 120). *Jurassic to Upper Cretaceous.*

Valves unequal. Hinge line long, straight, without teeth, but with numerous small, transverse ligament pits. Surface

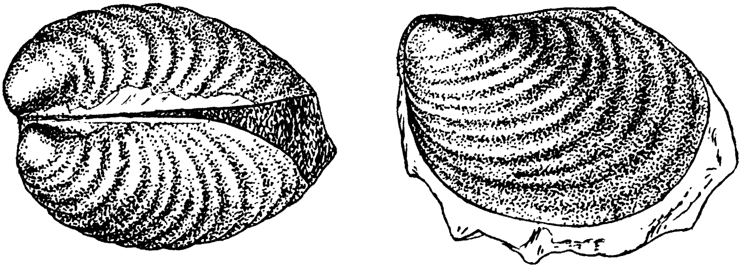


FIG. 120. — *Inoceramus barabini* Morton, from Montana. This pelecypod abounded in the shallow waters of the large ocean which cut North America into an eastern and a western continent during Upper Cretaceous times. *A*, hinge view of entire shell. The valves are separated posteriorly, and the beaks have been slightly displaced; the absence of articulating teeth renders such displacement, through the weight of sediment, very easy. *B*, outer surface of left valve of same specimen. Natural size of a small individual.

marked by coarse concentric undulations. This genus is especially characteristic of the Cretaceous.

1. Sketch (*a*) hinge view of combined valves; (*b*) outer surface of one valve. Label in sketches umbo, hinge line, growth ridges, oldest portion of shell, youngest portion, right valve, left valve.
2. Distinguish between umbo and beak.
3. What was the function of the row of pits along the hinge line?
4. Account for the slipping of one valve past the other in most specimens, so that the edges of the valves do not meet edge to edge. This slipping seldom occurs in such forms as Unio and Venus. Why?
5. How are pelecypod shells thickened? Illustrate by sketch.
6. Is the shell external or internal?

Pteria. *Devonian to present.*

Shell oblique, inequilateral and inequivalved, with the left valve more convex than the right. Hinge line long, bearing one or two small cardinal teeth and a long lateral tooth. Posterior ear wing-like, longer than the anterior. Sinus for the

passage of the byssus present under the right anterior ear. Ligament in a groove, partly internal and partly external. Only posterior adductor scar present in adults.

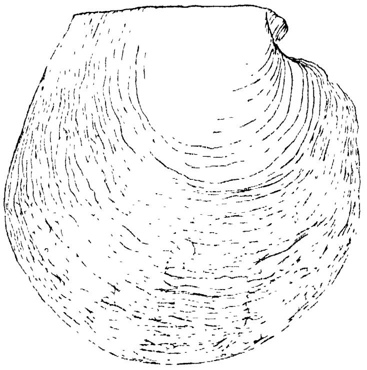


FIG. 121. — The "pearl oyster," *Meleagrina margaritifera*, from tropical seas. (× ½.)

Meleagrina (Fig. 121), a subgenus of Pteria, is of especial interest from the fact that one of its species, *M. margaritifera*, is the chief source of the white pearls of commerce. Pearl oysters are found especially in the East Indies. For the origin of pearls see page 273.

1. Sketch exterior of one valve, noting wing, ear, byssal sinus.
2. How are pearls formed?

Ostrea (Fig. 122). *Pennsylvanian to present.*

Shell irregular, attached when young to other objects by the left or larger valve. Beaks terminal. Left valve convex, right valve flat or concave. Structure of shell lamellar. External surface more or less distinctly ribbed. Teeth generally absent but hinge line broken by a triangular cavity for the ligament. Anterior adductor impression absent, posterior nearly central. No siphons present.

The shell becomes attached at the close of its free-swimming stage as soon as it settles to the bottom of the water. The mantle at the front (ventral) edge of the left valve when coming in contact with some foreign object secretes a cement (conchiolin) similar to the organic material within the shell itself.

Oyster shells are very often found to be completely riddled with small holes, the work of the boring sponge, *Cliona sulphurea.*

Fossil oysters are found in North America, Europe, and India. They are especially abundant in the Cretaceous of America and in the Tertiary of the coast states. A brackish

water form, living in tropical and temperate seas, the oyster thrives best in clear water close to the shore where the water is fresher than in the open sea.

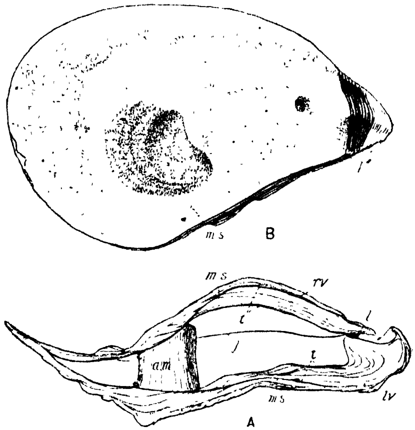


FIG. 122. — The common oyster, *Ostrea virginica* Gmelin, from the Atlantic coast of North America. *A*, longitudinal section through the valves showing the opening ligament (*l*), the closing or adductor muscle (*a.m.*), the anterior progression of the muscle scar (*m.s.*), which in this species is black, and the internal thickening of the shell (*t*); *j*, junction of the two valves; *l'*, ligament area; *l.v.*, left valve; *r.v.*, right valve. *B*, interior of right valve. (Both × ½.)

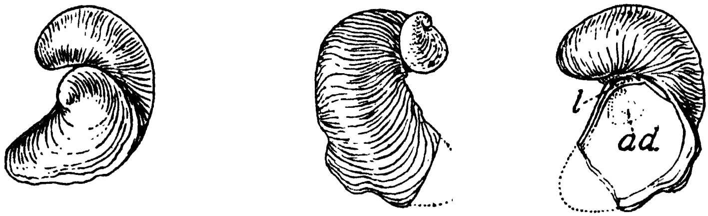
1. Sketch interior view of one valve, noting the characteristic V-shaped ligament area and the muscle marking.
2. Explain the action of the ligament in opening or closing the shell.
3. How does Ostrea differ from Nucula in (*a*) number of muscle impressions; (*b*) teeth?
4. Discuss the reason for the central location of the posterior adductor impression.
5. Is Ostrea attached or free during life? How can this be told from the shell?
6. In what kind of water does it usually live?
7. The oyster is a good example of adaptation to a sedentary life. How does this show in the shell?
8. Notice the difference in the shape and size of the valves. Why is this desirable?
9. Would such a heavy shell be satisfactory for the scallop (Pecten)? Why?
10. Sketch longitudinal vertical section of a valve, showing the progression of the muscle impression and thickening of the valve.
11. Why does Cliona bore into such shells as the oyster?

Exogyra (Fig. 123). *Upper Jurassic to Upper Cretaceous.*

Attached like Ostrea by the left valve but distinguished by the strongly twisted beak of this valve. Right or upper valve usually flat. Surface varying from nearly smooth to strongly

plicate. The name refers to the twisted beaks, from the Greek *exo*, out, + *gyros*, a curve.

Very characteristic of the Lower Cretaceous of Texas and of the Upper Cretaceous of both the western and eastern states.



A *B* *C*

FIG. 123. — The oyster-like pelecypod, *Exogyra arietina* Roemer, from the Del Rio clay of the Washita formation (Lower Cretaceous) of Texas. *A*, right valve shown in place within the larger left valve. (After Hill.) *B*, outer view of a slightly imperfect left valve. *C*, inner view of same; *ad.*, adductor muscle scar; *l*, ligament groove. Natural size.

E. arietina, at times, as in the Del Rio clay of the Texas Washita, occurs in enormous quantities, forming solid beds up to six inches thick (Fig. 124).

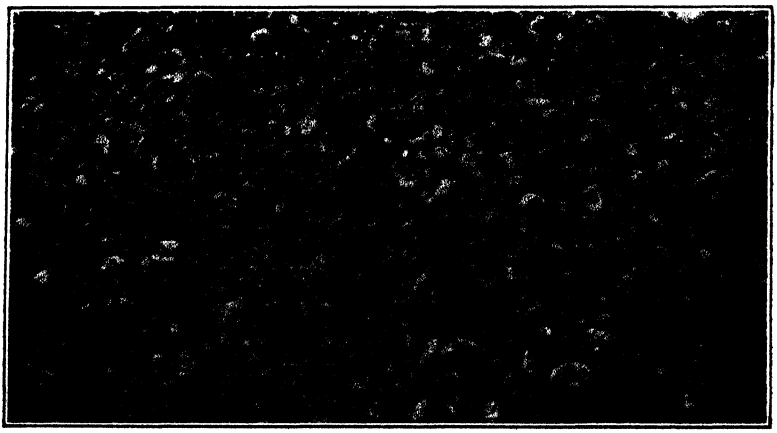


FIG. 124. — An oyster-like bed formed by *Exogyra arietina* in the ancient seas covering much of Texas during Lower Cretaceous (Del Rio) time. See Figure 123. (× ¼.) (From Hill.)

1. Name one similarity to Ostrea; one difference between the two forms.

2. At what time in the life of the individual Exogyra does it become attached to a foreign object? Reasons.

3. Sketch interior view of left valve, indicating muscle impression and ligament groove.

4. How is this known to be a pelecypod and not a gastropod?

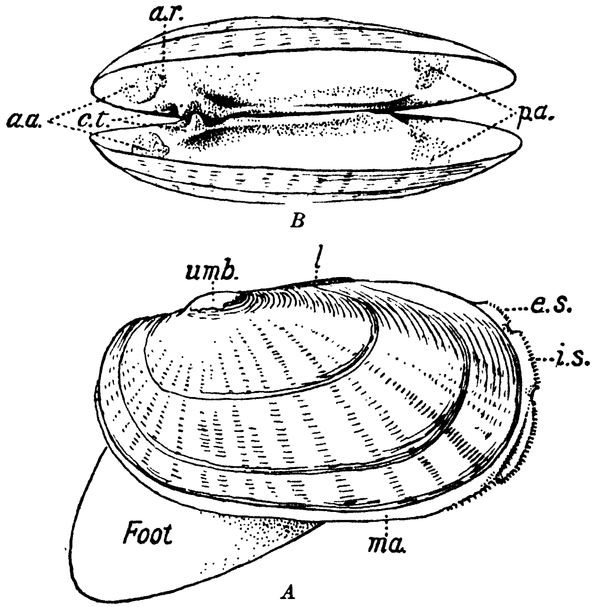


FIG. 125. — A fresh water mussel, *Unio luteolus* Lamarck, from Chisago Lake, Minnesota. *A*, exterior of living animal, left side. *B*, interior of the conjoined valves; *a.a.*, anterior adductor muscle scar. *a.r.*, scar of anterior foot retractor muscle; *c.t.*, cardinal teeth; *e.s.*, excurrent siphon; *i.s.*, incurrent siphon; *l*, ligament; *ma.*, mantle edge; *p.a.*, posterior adductor muscle scar; *umb.*, umbo, showing here its characteristic corrosion by the acids in the water. Natural size.

Unio (Fig. 125). *Jurassic to present.*

Valves of equal size, with a thick, brown, horny *epidermis* developed as a protection against the carbonic and humic acids in the fresh water as well as against the movement of the water itself. Shell thick, with a hinge line of heavy, indefinitely shaped

teeth. External ligament present. There are no true siphons, simply openings between the mantle edges for incurrent and excurrent water. The animal grows slowly and may live fifteen or twenty years. The name is derived from the Latin *unio*, a pearl; the shells are occasionally pearl-bearing.

These are the " river mussels " found at the bottom of lakes, ponds, or running streams in all parts of the world, more especially in the northern hemisphere. They rest erect with valves slightly gaping, partly buried in the mud and sand; if disturbed, the foot and mantle edge are drawn into the shell and the valves shut tightly.

The sexes are distinct. The eggs are fertilized within the body by spermatozoa introduced with the respiratory current; these fertilized eggs are passed into the cavities of the outer gills, where they are nourished by a secretion from their walls. The larvæ are thrown out through the exhalant siphon. The presence of these developing young causes the shell of the female to be more arched than that of the male.

There are more than one thousand living species. In the fossil state the genus is especially well represented in the Cretaceous of the Rocky Mountains.

1. Sketch interior view of one valve, noting teeth and sockets, pallial line, ligament and its place of insertion.
2. In the opening and closing of the valves what function was performed by (*a*) the teeth and sockets; (*b*) the ligaments; (*c*) the muscles?
3. What is the habitat of Unio? Its common name?
4. Why is the chitinous exterior of this form thicker than that of marine forms?
5. How do you account for the roughened surface at the umbo of most individuals?
6. What is the function of the teeth?
7. How can you usually tell the shell of a female Unio from that of a male?

Pecten (Figs. 126, 127). *Cretaceous to present.*

Shell nearly equilateral, with well-developed ears. Hinge line straight with a central pit for the insertion of the internal

ligament. Only one adductor muscle present. Surface usually marked with radial sculpture.

No siphons are present. Tentacles are present on the edges of the mantle. Of especial interest are the bright, bead-like *eyes,* arranged around the edge of the mantle. They possess cornea, crystalline lens, and retina. Experiment has shown them to be sensitive to changes in light and shade, though incapable of perceiving objects. They possibly sense the approach of an enemy by its shadow or by its movement in the water.

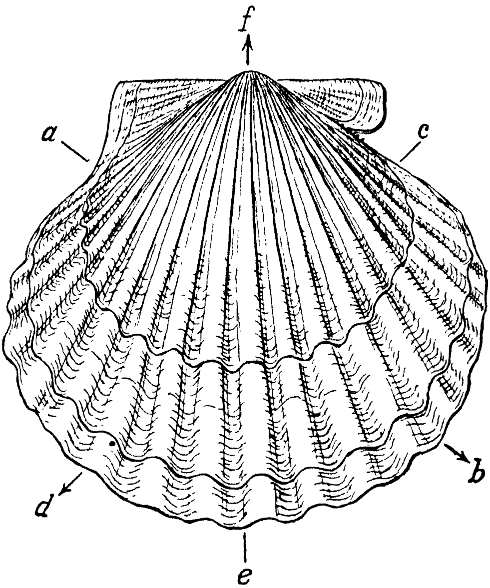


FIG. 126. — The right or lower valve of a two and a half year old scallop, *Pecten gibbus borealis* Say. (× ¾.) The arrows show how the scallop moves. When the animal forces the water out between the valves at *a* it moves in the direction of *b*, when out at *c* in the direction of *d*, when out at *e* in the direction of *f*.

The animal swims rapidly by flapping its valves together, thus ejecting water from the mantle chamber. When swimming, its hinge edge is usually directed backward and the propelling jet of water is forced from near the right and left ear alternately, thus acting like an oar in producing a zigzag course (Fig. 126).

It lives usually only a little over a year, spawning but once; very rarely does it reach a second spawning season. Its enemies are not many nor very destructive.

The *development* of Pecten has been carefully traced from the earliest shelled condition to that of the adult. The very young shell (the pro-

dissoconch), about 0.2 mm. in diameter, has a smooth surface, a very convex umbo, a curved hinge line with ten pairs of teeth fitting into corresponding sockets, with probably two adductor muscles and a non-prismatic shell structure. Immediately succeeding this stage and continuing until the shell reaches a diameter of about 1 mm., is the dissoconch (Fig. 127, *d*). It is characterized by a byssus, a byssal notch, formation of ears, a straight hinge line, a large active foot, prismatic structure of shell in at least the right valve, and a loss of the anterior adductor muscle. Later, at a diameter of about 1.25 mm. (the plicated stage) the number of plications normal to the adult appear all at once. In the adult the foot has almost entirely disappeared, and the shell structure is non-prismatic. The prodissoconch has usually been completely eroded in the adult shell.

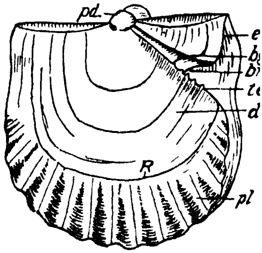


FIG. 127. — Plicated stage of a young scallop, *Pecten gibbus borealis* Say; outer surface of right or lower valve; the left valve shows slightly to the right. *b.g.*, byssal groove; *b.n.*, byssal notch; *d*, dissoconch; *er.*, ear; *pd.*, prodissoconch or earliest shell; *pl.*, plications; *R*, Rhombopteria stage (the Aviculopecten stage is reached when the plicated stage is about five times longer than represented here); *te.*, teeth. Size 1.4 mm. (Redrawn from Belding.)

Upon comparing the above changes with fossil adult shells, it is seen that the prodissoconch is exceedingly similar to the Ordovician Nucula, the dissoconch to the Silurian Rhombopteria (Fig. 127, *R*), allied to Pteria, the plicated stage to the Silurian Aviculopecten, the adult Pecten being known from the Pennsylvanian. The resemblances are so numerous and so close as strongly to suggest a true line of ancestry, since it is held as true among plants and animals that each individual in its growth to adulthood passes through stages of development which resemble adult individuals among its ancestors. This correlation of *ontogeny* — the individual animal's growth — with *phylogeny* — its ancestral history — is called the law of recapitulation.

The genus is of world-wide distribution. Three of the more common Atlantic coast American species used as food are, — *P. magellanicus*, New Brunswick to North Carolina, *P. gibbus borealis* of the New England coast, and *P. gibbus irradians*, which ranges from New Jersey to Texas. Other species

are much esteemed in Europe. Only the adductor muscle of scallops is eaten. Fossil forms are especially abundant in the Lower Cretaceous of Texas and the Upper Cretaceous of New Jersey.

1. When at rest Pecten lies upon its right valve. How does the right valve differ from the left?
2. Sketch right valve, both exterior and interior, indicating ears (anterior and posterior), umbo, ribs, growth lines, pallial line, byssal notch, muscle scar. Only one adductor muscle is present; is this the anterior or posterior?
3. Why is the byssal notch present?
4. Indicate with a heavier line upon your sketch the size of the shell at the end of one year. Why is this growth line so conspicuous?
5. Why are siphons, and hence a pallial sinus, not necessary in Pecten?
6. Mention two differences between Pecten and Venus.
7. How does it move from one place to another?
8. What is the common name of recent Pectens?
9. How does the shell usually give indication of the age of the animal?
10. How does the living Pecten breathe?
11. What portion is eaten by man?
12. What need has the animal of so large an adductor muscle?
13. Where are the eyes? Why? Can most pelecypods see?
14. Give briefly the development of the shell from the early prodissoconch stage to the adult.
15. Parallel this development with fossil forms.
16. State the law of recapitulation.
17. How are the plications formed?
18. Distinguish Pecten from Pteria.

Teredo (**" ship-worm "**) (Fig. 128). *Jurassic to present.*

Shell much reduced, globular, with valves gaping at both ends. Pedal muscles attached to a long, narrow plate beneath the umbos.

The animal lodges at the inner end of a long burrow which it has formed in wood. This burrow is lined by a shelly tube, secreted by and covering the long conjoined siphons of the animal which extend from between the valves out to the open end of the burrow. The free extremities of these siphons are protected by two small, movable, calcareous plates, the palets.

The valves bear rows of microscopic "teeth" like those of a file, with which the animal makes its way into wood. With the foot attached to the wood, the animal gives itself a rocking motion by alternate contractions of the anterior and posterior adductor muscles, and the valves rasp away the wood as a fine dust. This is swept into the mouth and constitutes a part of the food of the

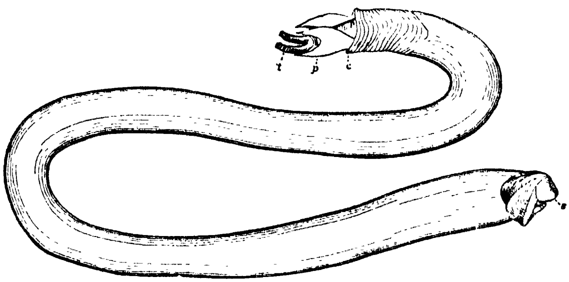


FIG. 128. — The "ship-worm," the pelecypod, *Teredo navalis* Linné, from the coast of Massachusetts. In life a tube of lime carbonate encases the animal from the shell (*s*) to the collar (*c*). *c*, collar; *p*, palets; *s*, shell; *t*, siphons. (From Verrill and Smith.)

animal along with the Infusoria and other minute planktonic organisms drawn in with the water through the branchial siphon.

Teredo navalis is abundant on American and European shores, doing great damage to submerged timbers. Various methods of metal sheathing, as well as impregnation with poisonous substances such as creosote, have been found effectual to a large extent. At the present time, though ships are protected against the attack of the ship-worm, it still constitutes a menace to harbor construction. A sudden temporary increase of salinity of the water in San Francisco Bay caused an outbreak of ship-worm, which in four years (1917–1921) worked destruction on wharves and jetties estimated to cost 25 million dollars. The various species of Teredo are nearly always found within some hard vegetable substance.

1. Sketch exterior of one valve.
2. What is the food of Teredo? How is this procured?
3. Does it digest the wood eroded in the formation of its burrow?

CLASS C. GASTROPODA

Type of class, *Busycon canaliculatus* (Linné) (Figs. 129–131). This species is one of the largest gastropods on the Atlantic coast, often attaining a length of six inches. It is especially abundant on sandy bottoms, at or below low tide level, where

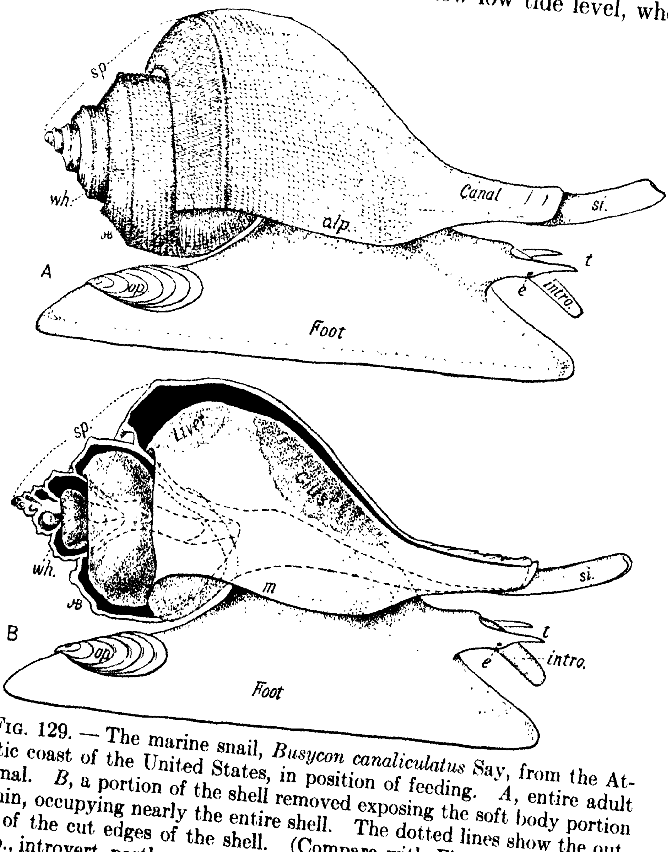


FIG. 129. — The marine snail, *Busycon canaliculatus* Say, from the Atlantic coast of the United States, in position of feeding. *A*, entire adult animal. *B*, a portion of the shell removed exposing the soft body portion within, occupying nearly the entire shell. The dotted lines show the outline of the cut edges of the shell. (Compare with Figure 130.) *e*, eye; *intro.*, introvert, partly extended; *m*, mantle edge; *o.lp.*, outer lip of shell; *op.*, operculum; *si.*, siphon; *sp.*, spire of shell; *t*, tentacles; *wh.*, whorl or revolution. *A* shows a shell of six whorls. (× ⅔.)

it may be found slowly plowing its way through the sand or lying with the foot partly buried. It ranges from Cape Cod southward, favoring especially the New Jersey coast and Long Island Sound. It has lived along the Atlantic coast since Pliocene times.

The soft body of the animal is inclosed within a single calcareous shell, somewhat pear-shaped and consisting of six coils or whorls. At one end the shell is prolonged into a slender, half cylindrical canal. As the animal moves the canal projects forward and the apex of the whorls backward. Thus it is seen that the canal is at the anterior end of the shell and the apex of the whorls at the posterior.

Viewed in the position assumed when feeding, there is visible externally a head with two tentacles or feelers and a large foot, which forms the whole ventral aspect of the animal. When the shell is removed, the large elongated body mass, the visceral spiral, is found to extend backward from the upper side of the foot. This, like the shell in which it was lodged, is twisted into a coil. A delicate colorless *mantle* surrounds the visceral spiral, fitting closely both anteriorly and posteriorly but arching away in the middle, leaving a wide mantle (pallial) cavity. Marginally, the mantle is thickened and at one place is produced into a tube, the *siphon*, open along one side; this extends out through the canal of the shell.

The organ of **respiration** is the single *gill* which lies on the wall of the mantle cavity. This is a leafy expansion of the mantle, consisting of a row of flattened tubes bound together at the base by a common axis like the leaves of a book. A fresh supply of water is forced through the siphon into the pallial cavity, and hence the gill is constantly bathed in water abundantly supplied with oxygen. (The structure of the gill is similar to that in Venus, Fig. 117.)

The impure blood from the body is brought to the gill by a large vein and is forced into these gill tubes, through the thin wall of which the carbon dioxide carried by the blood is exchanged for the oxygen carried by the water. It is probable that the function of respiration

is likewise in part performed by that portion of the mantle surface which is exposed to the water, as in most mollusks this portion is crowded with thin-walled capillaries.

The **digestive system** begins with the mouth situated at the anterior end of the alimentary canal. Usually, however, the mouth is not visible, being pulled back into the œsophagus. The peculiar mechanism which accomplishes this withdrawal of the mouth is called an *introvert;* it works like the pulling in of the finger of a glove by a thread from within. During its invagination the wall of the digestive canal is folded twice on itself, thus pulling inward its anterior extremity, the mouth. During evagination this fold partially straightens out and the mouth is thus pushed out to occupy an anterior position.

The mouth leads into the buccal cavity, an enlargement of the digestive canal which in turn opens into the œsophagus. The muscular walls of this cavity bear the apparatus for mastication, two small chitinous jaws or mandibles, and the *radula,* a thin membranous ribbon bearing transverse rows of many tiny chitinous teeth. The radula is borne on a cartilaginous support, the odontophore, furnished with protractor and retractor muscles by whose action the radula may be sent out through the mouth and may work to and fro like a rasp upon the animal's prey. The extrusion of the mouth through the agency of the introvert carries with it likewise the buccal cavity with its included radula, thus placing the animal in position for feeding.

Into the buccal cavity open the salivary glands which secrete a mucus with little or no digestive action. Food passes from the buccal cavity through the œsophagus to the stomach, a simple enlargement of the digestive canal. The *liver* is a soft brownish mass, more or less completely surrounding the stomach and forming a large part of the coiled mass of viscera. It is the chief organ of digestion, secreting a ferment which pours into the stomach. From the stomach the food enters the intestine through whose walls it is absorbed and from whose posterior extremity the waste products are discharged into the mantle cavity, whence they are borne outside the body by the respira-

tory current of water as it leaves the gills. Busycon is carnivorous.

The main organ of the **circulatory system** is the dorsal *heart* inclosed in the pericardium at the base of the gill; it consists of two chambers, one auricle and one ventricle. From the heart, the blood passes through arteries, open sinuses, and veins, thus distributing food and oxygen all along its course. The blood of Busycon is colorless. The chief organ of *excretion* is the kidney — essentially a sac lined with secretory epithelium, which discharges the waste products which it collects into the mantle cavity, whence it is washed out of the shell.

The **nervous system** consists of paired cerebral and pleural ganglia situated over the œsophagus, paired pedal ganglia situated in the foot, and paired visceral and abdominal ganglia. Nerve connectives unite all these ganglia; those joining the pleural and visceral ganglia are crossed, producing an 8-shaped loop.

Sensory cells are present over the whole surface of the mantle, but in certain areas, mostly in the anterior regions of the body, they become specialized into definite sense organs. The sense of touch is especially resident in the lower surface of the foot, which is covered by a network of fine nerves, and also in the tactile tentacles. The tentacles function also in the sense of smell.

The *osphradium*, with function possibly combining taste and smell, is a ciliated region specialized by an accumulation of sensory cells, and situated at the outer edge of the gill, where the current of water supplying the gill must pass over it. *Otocysts*, the organs of balance, are located at the base of the tentacles; they are hollow sacs containing a liquid and some concretions and with ciliated walls possessing sensory cells. The organs of sight are two small sessile *eyes* upon the outer edge of the tentacles; they are provided with a protecting cornea, a light-focusing lens, and a retina with pigmented and sensory cells. These eyes by condensing the rays give the animal a definite perception of the direction of light.

Two of the more important **muscular** areas are the foot and the columellar muscle. The *foot* is a powerful mass of muscular tissue with a flat lower surface adapted to creeping. Successive waves of movement pass over this surface wherein successive points are raised, passed forward and again planted and thus effect the creeping movement of the whole foot, as in walking a man raises one foot, pressing the other at the same time against a resistant surface. The animal is held in its shell by the contraction of the *columellar muscle* which extends from the concave right side of the body to the columella to which it clings, its place of attachment moving spirally forward with the growth of the shell.

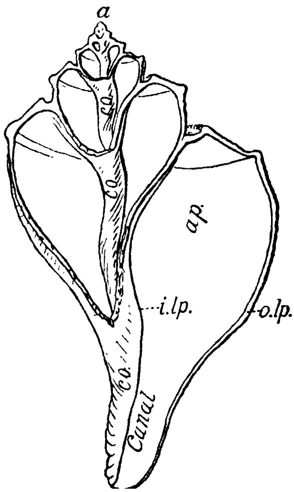


Fig. 130. — The shell of *Busycon canaliculatus*, with a portion broken away showing the method of coiling. *a*, apex of spire, the position of the protoconch when preserved; *ap.*, aperture of shell; *co.*, columella; *i.lp.*, inner lip; *o.lp.*, outer lip. (A small individual × $\frac{3}{4}$.)

The **shell** is formed by the mantle as in Pelecypoda (p. 268); the surface irregularities of the shell merely reflect corresponding surface irregularities of the mantle. The closely wound whorls form an elongate cone whose base is the aperture of the shell, and whose apex, the oldest portion of the cone, corresponds to the umbo of pelecypods. The axis of union of the whorls is the *columella* (Fig. 130, *co.*). It forms the inner boundary of the aperture called the columellar or inner lip in opposition to the thin outer lip. The *operculum* is a small accessory shell, a flat oval plate, borne on the foot, which on the withdrawal of the head and foot into the shell closes the aperture (Fig. 129, *op.*).

The **sexes** are distinct. The eggs are fertilized within the body of the female and are laid in great masses together with abundant nutritive material. In Busycon these masses of eggs

and food are in the form of a long series of disk-shaped parchment-like capsules, like checkers on a string (Fig. 131). There are on the average 70 capsules in each string and each capsule contains about 50 embryos surrounded by much albuminous fluid which serves as nourishment during the growth from eggs to tiny shelled individuals. These egg cases are numerous on the beaches in spring and early summer. So small is any one indi-

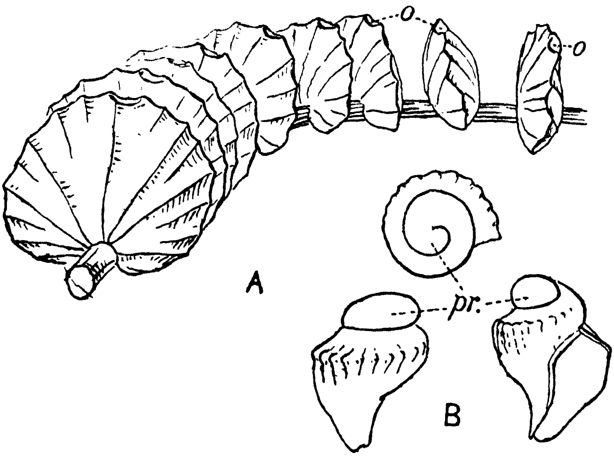


FIG. 131. — *Busycon canaliculatus.* *A*, portion of a string of egg capsules. Natural size. *B*, three views of the young shell (4 mm. long) when ready to leave the capsule by the opening *o* in *A*. Top sketch shows view looking upon apex of spire. The first or smooth whorl is called the *protoconch* (*pr.*).

vidual's chance of surviving the various unfavorable conditions and the many enemies surrounding it that it has been estimated that about one in 20,000 of the tiny embryos reaches maturity. The first shell of the larval stage forms, when preserved, the extreme tip of the adult shell. It is called the *protoconch* and consists of a single smooth volution with no anterior canal; it suggests the shell of Natica in appearance (Fig. 131, *pr.*). This naticoid stage is one that very generally occurs among gastropods and one that recalls the characters of early gastropods, such as *Straparollina remota* of the Lower Cambrian, which is

perhaps close to the protogastropod, the earliest gastropod ancestor.

Just before the animal breaks out from the egg capsule a second whorl is added which develops tubercles on its shoulder angle and whose lip begins to extend into the anterior canal so characteristic of the adult. The growth of this canal tilts the plane of coiling of succeeding whorls at an angle to the plane of the first whorls. Hence the protoconch has an oblique appearance in the adult.

1. What is the present habitat of Busycon? Its geologic range?
2. As it moves, which way does the spire point?
3. Describe the respiration of the animal.
4. What does it eat? How is this procured and eaten? How digested?
5. Outline briefly the circulation of the blood.
6. What sense organs does Busycon possess? Where situated?
7. How does the animal move?
8. How is the body held in the shell?
9. What does the word gastropod mean and why applied to this class?
10. Sketch (*a*) shell, looking into aperture and with spire pointing upwards; (*b*) section of shell from tip of spire to siphon. Label whorl, columella, inner and outer lips, spire, oldest portion of shell.
11. Sketch the entire body removed from the shell. Indicate mantle, siphon, spire, columellar muscle, liver, operculum, foot.
12. What is the function of the operculum?
13. Did the body of the animal occupy the whole or only a portion of the shell?
14. How was the shell built?
15. Are the sexes separate or united in one individual?
16. How are the eggs laid? How many at a time? What proportion of these reach maturity?
17. Define the protoconch. What does this indicate as to the past history of Busycon?
18. How would an internal mold of the shell be formed?

General Survey of Class Gastropoda

Gastropoda are with few exceptions characterized by the possession of a distinct head, creeping foot, and single mantle which in most forms secretes a spiral or saucer-shaped shell.

The head, except in a few degenerate forms, bears tentacles and eyes.

Nearly all gastropod shells are more or less coiled, resulting from the more rapid growth of one side of the body and its mantle. It is usually the left side which grows more rapidly than the right, producing a dextral (right-handed) coil. If, when the shell is held apex up with the aperture towards the observer, the aperture is on the right, the coiling is said to be *dextral;* if on the left, it is *sinistral.*

In addition to this external asymmetry produced by the coiling of the shell, gastropods are characterized, at least at some period of their development, by an internal asymmetry resulting from a torsion of the body. In this the digestive canal, which in the very young embryo (up to the trochosphere stage) has mouth and anus at opposite ends of the body, becomes flexed upon itself and twisted upward, bringing the anus to the anterior end, above the mouth. This torsion is connected with the increasingly great development of the foot and the enlargement of the main visceral mass, the liver and reproductive organs. In the train of this torsion follow various displacements of the gill and nephridium on the shortened side, and typically their atrophy and disappearance. In many gastropods this twisting of the body involves likewise the nerve connectives, which thus become crossed.

In the *pulmonates*, the air-breathing snails, which are mainly terrestrial or of a fresh-water habitat, there are usually no gills. The mantle cavity becomes completely closed except for a small opening, and functions as a lung.

The water for respiration passes in through a fold of the mantle lying in the anterior notch of the shell, or through the canal, where this is present, and out above, past the anus. If a posterior canal is present it passes out through this.

The heart consists usually of but two chambers, an auricle and a ventricle; rarely, as in Haliotis, are there two auricles and a ventricle. The blood is usually colorless. It is red in most species of Planorbis in which hemoglobin is diffused in the plasma, and bluish in *Polygyra albolabris* owing to the presence of hæmocyanin, an albuminoid containing copper.

The heart of adult gastropods beats between 30 and 100 times a minute, but during hibernation not more than twice a minute. In young gastropods the number of beats may reach 150.

Experiment indicates that *touch* and *smell* are the most acute senses of gastropods. It is almost exclusively by the sense of smell that food is found. This sense varies in acuteness in different gastropods. Its usual range does not exceed one inch, though some carnivorous marine forms (*e.g.*, Nassa) can thus detect objects at a distance of more than six feet. It has been shown that *Polygyra albolabris* can locate food when covered from sight, even at a distance of 18 inches. *Natica heros* will go in a straight line to a dead crab.

Experiment has also shown that to aquatic gastropods the form of objects is indistinguishable, and this is probably true likewise of terrestrial species, for it has been shown that *Polygyra albolabris*, the common land snail, has so little perception of forms that it often creeps directly against an object, changing its course only when the tentacles touch it. The same animal is entirely unaffected by any noise which does not actually jar its body.

A large percentage of the gastropods are herbivorous. Of the marine forms the vegetable feeders have as a rule the outer lip of the shell aperture entire (exceptions are Natica, the Scalariidæ, etc.), while the carnivorous forms have this lip notched or drawn out into a canal (as Murex, etc.). Most of the former likewise have many and small teeth upon the radula, while in the latter they are few but strong. Gastropods drill holes in the valves of pelecypods and other mollusks by means of the radula which is aided by an acid secretion of the alimentary canal.

Sometimes the inner parts of the whorls coalesce into a *columella.* When they do not thus unite but leave a central tubular cavity, the opening of this cavity below is called the *umbilicus.* In some cases the inner edge of the mantle is reflected back over the inner edge of the aperture, and secretes a shelly growth beneath it which partially covers the umbilicus and is called the *callus.*

In many forms the mantle protruding from the shell aperture is reflected back over the shell to such an extent that it covers more or

less of its external surface as in Cypræa, and this reflected portion may secrete a coating of enamel over the part of the shell on which it lies. The shell in these forms becomes thus more or less inclosed within the soft body portion, a process which attains such an extent in certain forms representing offshoots from various groups (*e.g.*, Marseniidæ from the Streptoneura, the slugs from the Pulmonata, the sea-hares from the Opisthobranchia, etc.) that the animal appears to be quite naked. In these the mantle not only covers the shell but its edges are fused together over the top. The shell accordingly, having almost ceased to be of use as a protection, degenerates into a small plate, appearing entirely unlike the ordinary gastropod shell. Finally the shell disappears entirely in the nudibranchs, some of the pteropods, and some of the air-breathing gastropods.

As the shell is the only part preserved in fossil forms, our knowledge of the characteristics of extinct species and their relationship to one another and to living forms is based largely on considerations of shell outline and ornamentation, *i.e.*, on the presence or absence of such shell characters as columella, umbilicus, callus, etc. The operculum is commonly of corneous nature and is hence rarely preserved in the fossil state. For a consideration of the protoconch see page 292.

Busycon, with its twisted nerve connectives and separate sexes, is a type of one of the two subclasses of the gastropods, the Streptoneura; while Creseis, with its untwisted nerve connectives and united sexes, is an example of the Euthyneura. Under the Streptoneura belong Pleurotomaria, Bellerophon, Fissurella, and Turritella, while under the Euthyneura, Creseis and Tentaculites are included with the order Opisthobranchia, Helix with the second of the two orders, the Pulmonata. Gastropods are known from the Cambrian to the present, though in abundance only since the Ordovician.

Derivation of name: Greek *gaster*, stomach, + *pous* (*pod*), foot. The stomach is directly above the creeping foot in most gastropods.

Pleurotomariidæ (Fig. 132). *Ordovician to present.*

In this family of gastropods the outer lip of the aperture is cut by a slit resulting from a corresponding notch in the mantle.

Through this posterior notch are expelled the digestive waste and the respiratory water; the incoming water and the food are thus kept unpolluted. From the slit in the shell, a *slit band*, marking the progressive closing of the slit during the growth of the shell, extends backward; around this the growth lines bend obliquely. Name from Greek *pleura*, side, and *tomarion*, a cut.

Though an abundant fossil form, with over 1100 species known, there are but five living species.

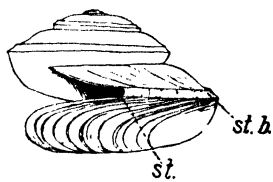


FIG. 132. — One of the Pleurotomariidæ gastropods, *Eotomaria supracingulata* Billings, from the Stones River formation (Lower Ordovician) of Illinois. *st.*, slit in outer lip; *st.b.*, slit band. (From Ulrich.)

1. Sketch view showing aperture and spire; label spire, whorls, aperture, slit.
2. To what is the slit due?
3. Of what advantage is the slit to the animal?

Bellerophon. *Ordovician to Permian.*

Globular, with the earlier whorls concealed by the later ones. Umbilicus present on each side. Aperture sub-circular with a deep median slit, comparable to that present in the members of the Pleurotomariidæ, which as it progressively closes with the growth of the shell, arches into a keel.

Especially abundant and widespread in the Mississippian and Pennsylvanian of North America.

1. Sketch (*a*) view looking directly into the aperture, (*b*) side view showing umbilicus. Indicate aperture, umbilicus, keel, slit band.
2. How is the umbilicus formed?
3. A section through the shell shows several whorls. Why are the earlier whorls not visible in the unbroken specimen?
4. What characters indicate that this is not a coiled cephalopod shell?
5. What caused the slit band? Its use?

Fissurella (Diadora) (See Fig. 133). *Living.*

The mantle and shell of this keyhole limpet are pierced by an oval hole just over the summit of the visceral cone. This hole in the mantle functions as an anal siphon, for it gives passage to

the digestive waste and to the water from the gills, which have been poured into the mantle cavity. It thus corresponds to the slit of the Pleurotomariidæ (Fig. 132, *st.*), to some of the posterior holes in the Pacific coast earshell (Haliotis), and to the posterior canal of such shells as Cypræa. The hole first appears as a notch in the border of the mantle, as in Haliotis, but is surrounded by the later growth of the mantle and resultant shell. From this aperture are derived both the Latin and common names (Latin *fissurella*, a little hole).

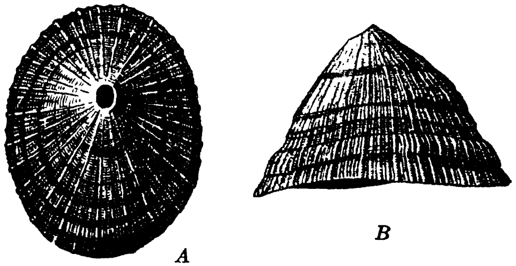


FIG. 133. — The keyhole limpet, *Fissuridea alticosta* Conrad, from the Miocene of Maryland. Natural size. *A*, dorsal view. *B*, side view. (From Martin.)

The fossil forms are now referred to Fissuridea, ranging possibly from the Carboniferous.

1. Sketch side view, noting the anal aperture.
2. What function did the anal aperture subserve?
3. In regard to this aperture compare Fissurella with Pleurotomaria, Bellerophon, and Haliotis.
4. Compared with Crania, how do you know that Fissurella is a gastropod and not a brachiopod?

Turritella (Fig. 134). *Triassic to present.*

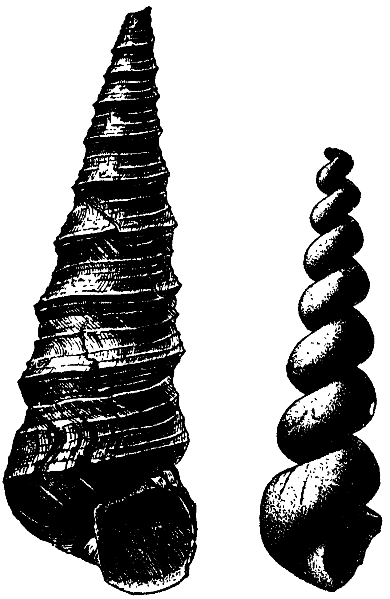
Shell shaped like a tapering tower or turret, suggesting the name (from the diminutive of the Latin, *turris*, a tower). No umbilicus present. There is no siphon and hence the aperture of the shell is entire, *i.e.*, not produced into a canal.

It is represented by many species in the Cretaceous and Tertiary of North America, such as *T. mortoni* of the Eocene of the Atlantic and Gulf coastal plain.

The terminals of various genetic lines of Turritella are found in the species of the genus Vermicularia (Tertiary to the present).

In this genus, the earlier, younger, whorls are like Turritella, while the later, adult, whorls are uncoiled and somewhat twisted.

1. Sketch (*a*) side view showing the elongate spire and the aperture; (*b*) side view of an internal mold. Note spire, whorls, aperture.
2. How much of the shell did the body of the animal occupy?
3. How does this compare with the portion of the shell filled by the internal mold?
4. How is an internal mold formed?
5. In what kind of rocks are the best internal molds found?
6. What information about the soft body of the animal does this form of preservation give?
7. Show that Vermicularia is descended from Turritella.
8. Given only the irregularly coiled portion of Vermicularia, show that it was secreted by a gastropod and is not (*a*) a worm-tube like Serpula nor (*b*) a siphonal tube like that of Teredo.
9. Why is Turritella placed in the class Gastropoda?
10. What according to derivation does the word gastropod mean? Why applied to the members of this class?
11. How is the gastropod shell built?
12. When the animal moves which way does the spire point?



A *B*

FIG. 134. — *Turritella mortoni* Conrad, from the Eocene of Maryland (× ¾). *A*, shell entire except for the missing apex of the spire. *B*, the internal mold (or mud filling) of the shell. (After Clark and Martin.)

Creseis (Clio) (Fig. 135). *Tertiary to present.*

Creseis is a tiny gastropod, often shaped like a narrow, elongate cone, about an inch long. It occurs in immense swarms in northern and southern seas, swimming in the open ocean by flapping movements of the fin-like lobes of its foot. It forms much of the food of whales.

It differs from Busycon in its symmetrical, uncoiled body and shell, and in the expansion of the foot into the two symmetrical fins used in swimming.

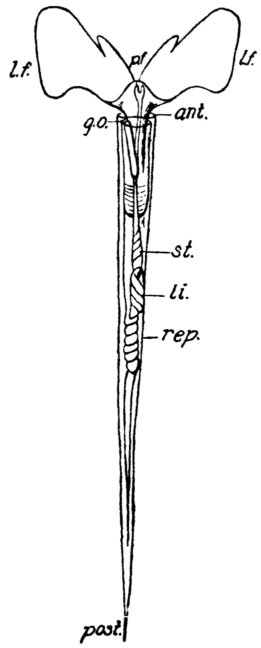


FIG. 135. — The gastropod, *Creseis* (*Clio*) *acicula*, ventral view; this has a universal distribution. Much enlarged. *ant.*, anterior margin of shell; *g.o.*, genital opening; *l.f.*, lateral fin, — the wing-like lateral lobe of the foot; *li.*, liver; *p.f.*, posterior fin, — the median posterior lobe of foot; *post.*, posterior end of shell; *rep.*, reproductive gland; *st.*, stomach. (Redrawn from Lankester's Zoölogy after Souleyet.)

The shell is thin, in the form of a tapering tube, without transverse septa. From its larger and open end project the two large wing-like lobes of the foot. This open end is anterior; there is no distinct head. A mantle surrounds the body and secretes the shell.

There is a general symmetry of the body organs resulting from a second torsion of 180° in a direction opposed to that of the original torsion of other gastropods; the primitive torsion appears in the course of the animal's development. This secondary symmetry is most manifest in the nervous system. The visceral connectives are not crossed as they are in Busycon, and the nerve elements are concentrated in the anterior region, around the œsophagus.

The two sexes are united in one individual.

Creseis is one of the *Pteropoda*, a group formerly differentiated among the Gastropoda, but now usually broken up and scattered among various divisions of the tectibranchs — a suborder of the Opisthobranchia. They were formerly segregated on the basis of their common possession of a foot transformed into two wing-like fins and of their lack of a distinct head.

1. What characters do Creseis and the other members of the old class Ptero-

poda possess in common which distinguish them from the rest of the gastropods?

Tentaculites (Fig. 136). *Ordovician to Devonian.*

The shell is thick-walled and conical, tapering posteriorly to an acute apex. The surface of the shell is banded with raised parallel rings.

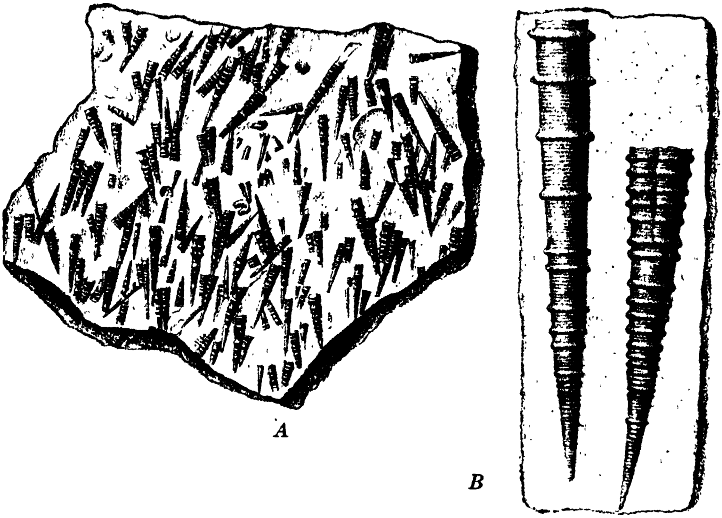


FIG. 136. — *Tentaculites gyracanthus* Eaton. A straight gastropod (conularid) from the Upper Silurian of New York. *A*, block of limestone showing their abundance (natural size). *B*, two individual shells (× 4), the smaller one has been slightly crushed. (After Hall.)

This is an extinct genus exceedingly abundant in the Silurian and Devonian.

Tentaculites, Hyolithes, Conularia, etc., are genera of problematic relationship occurring abundantly in the Paleozoic. They are often raised into a distinct class of the phylum Mollusca, the *Conularida.* Though the occasional presence of transverse septa has somewhat suggested relationship with the Cephalopoda, still their shell is most similar to that of Creseis, and hence they are undoubtedly most closely akin to the Gastropoda among classes of living mollusks.

1. Sketch side view, noting the long, uncoiled tube with its ring-like ornamentation.

2. Why is this shell, and others of similar structure, often raised into a distinct class?

Helix (See Fig. 137). *Eocene to present.*

This is a pulmonate gastropod. The mantle cavity contains no gill and itself functions as a lung for breathing air, since its walls are traversed by blood vessels. The animal is hence terrestrial in habitat.

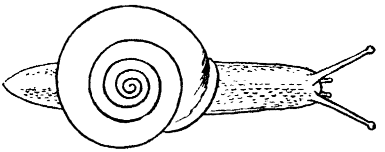


FIG. 137. — The common land snail, *Polygyra albolabris*, from New York State. (× ¾.) This is closely allied to Helix. Dorsal view of creeping animal, showing the coiled calcareous shell and the active feelers or tentacles; each of the two longer tentacles terminates in an eye. Note that the coil of the shell is posterior (compare with Figure 140). (Redrawn from Simpson.)

The genus and its subgenera include more than 4000 species.

1. Sketch side view showing aperture and spire, labeling spire, aperture, whorls.

2. What modification has the animal undergone that enables it to live upon land?

CLASS D. SCAPHOPODA

The Scaphopoda are characterized by an elongate, bilaterally symmetrical body which thus looks worm-like. This body is inclosed in a tubular, calcareous shell which is curved and tapering, and open at both ends, and is secreted by the mantle lobes, which are joined in the mid-ventral line except at the posterior and anterior ends. The body is attached to the posterior part of the shell by muscles. The concave side is dorsal. The larger end is anterior; through it the foot can be protruded and used for burrowing in the sand and mud. In this end of the shell, likewise, is the short proboscis or "head," which bears the mouth.

The structure of the body is very simple. There are no special circulatory organs, no gills, respiration being effected by the whole mantle, and the head bears no eyes. Into the posterior aperture of the shell is drawn the water used for breathing, and

through it is discharged the body waste. Affinity of scaphopods with the gastropods is indicated by their possession of a radula, a mandible, and a somewhat similar nervous system.

The somewhat similar tubular shells of gastropods and cephalopods may be distinguished from these by the fact that they are always closed at one end.

Scaphopods are marine and live embedded in mud and sand, usually at great depths. They range from the Ordovician to the present. There are twelve known genera and over 300 species. Dentalium, the tooth shell, ranges from the Eocene to the present (Fig. 138). The family Dentaliidæ extends back into the Ordovician.



Fig. 138. — A scaphopod, *Dentalium attenuatum* Say, which lived in the seas covering eastern Maryland during the Miocene. *ant.*, anterior aperture; *dor.*, dorsal side of shell; *post.*, posterior aperture. Length of shell 2.3 inches. (After Martin.)

1. Sketch side view. Label mouth end, anal end.
2. Distinguish a scaphopod from a straight gastropod, like Tentaculites.

CLASS E. CEPHALOPODA

Type of the class, *Nautilus pompilius* (Fig. 139).

The pearly Nautilus lives in moderately shallow or deep water in the South Pacific, usually creeping about on the bottom. The body is inclosed in a coiled shell, secreted by the mantle, from which project the head and tentacles when the animal is moving and into which they may be withdrawn for protection. The appearance of Nautilus, with its expanded tentacles surrounding the head, is similar to that of the disk of a sea-anemone. The shell consists of an elongate cone coiled in one plane and is divided by transverse partitions (the *septa*) into a series of chambers. The soft body of the animal is lodged in the wide end of the cone in front of the last formed septum; this cup-like chamber

in which it lies is called the *living chamber*. An extension of the body, the *siphon*, passes backward from the living chamber, through perforations in the septa; it thus maintains connection with the earliest formed chambers in the apex of the shell.

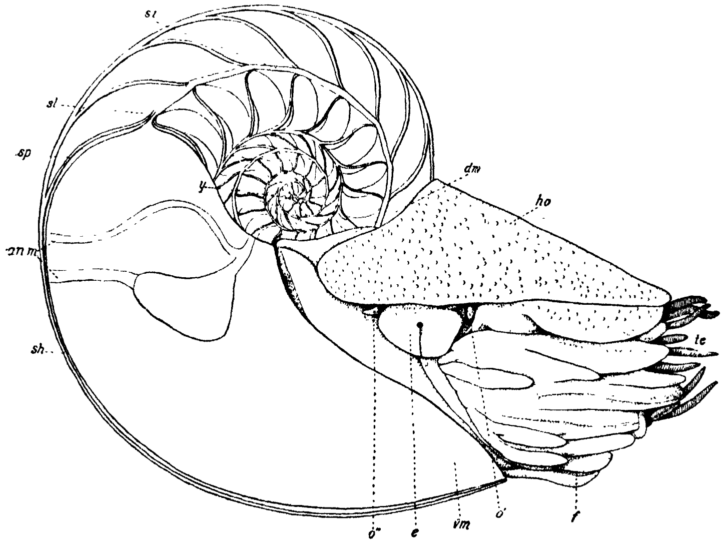


FIG. 139. — *Nautilus pompilius*, from the Philippine Islands (× ½). The animal is seen from the right side, the right half of the shell having been cut away. *an.m.*, annular muscle which holds the body of the animal in the shell; the posterior portion of the muscle is attached at the junction of the last septum with the shell; *d.m.*, dorsal portion of mantle; *e*, eye; *f*, funnel; *ho.*, hood, which, like the operculum of gastropods, may be drawn in against the aperture to close the shell; *o'*, *o''*, anterior and posterior ocular tentacles; *si.*, siphon, the fleshy prolongation of the mantle extending backward through the empty chambers; *sl.*, siphuncle, the shelly covering of the siphon; *sp.*, septum, one of the transverse partitions of the shell; *te.*, tentacles; *v.m.*, ventral portion of mantle; *y*, earliest formed portion of the calcareous shell. (Redrawn from Griffin.)

This *siphon* is really just an extension of the cœlome or body cavity of the animal, a tubular extension opening from the posterior portion of the cœlome. An artery extends through its entire length, finally ending openly. Though the siphon narrows where it passes through each septum, yet its cavities are not effaced.

The function of the siphon is unknown. Some have supposed it to be a hydrostatic organ, assisting the animal to rise and sink through the water. And some have considered that whatever be its function, it is in Nautilus a vestigial structure which has become progressively reduced during the course of evolution of the Nautiloidea.

When *creeping* on the sea bottom the tentacles surrounding the mouth are applied to the surface over which the animal is traveling and movement is effected by them (Fig. 140). In this natural creeping position the soft body is nearly horizontal, though curving upward posteriorly. The head is anterior, the siphuncle is posterior, the funnel is ventral, and the coil of the shell is dorsal.

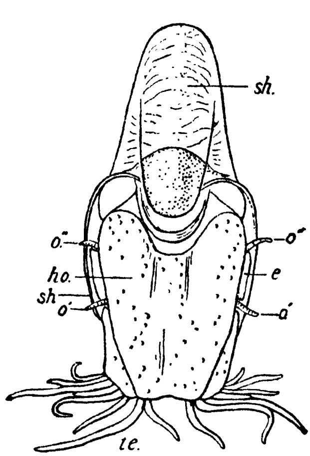


FIG. 140. — *Nautilus macromphalus*, creeping upon a horizontal surface. Note that the coil of the shell is anterior (compare with Figure 137). *e*, eye; *ho.*, hood; *o′*, *o″*, anterior and posterior ocular tentacles; *sh.*, shell; *te.*, tentacles. (Redrawn from Lankester's Zoölogy after Willey.)

Shell. — The adult shell possesses about two and a half whorls; the exterior is marked with alternating bands of reddish brown and white. Internally, the shell as previously stated is made up of a series of chambers separated by septa. Pelseneer suggests that each septum shutting off a chamber "is formed during a period of quiescence, probably after the reproductive act, when the visceral mass of the Nautilus may be slightly shrunk." The thin glandular skin covering the posterior portion of the animal secretes the septum, probably first as a membrane of conchiolin, which later becomes impregnated with lime. The lines of union of these septa with the outside walls of the shell are called *sutures*. These are invisible externally except where the outer surface has been worn off. (Compare with Fig. 143, *su.*) The sutures are slightly undulating, possessing a small ventral *lobe*

(an undulation convex away from the aperture) and broad lateral *saddles* (undulations convex toward the aperture). (Compare with Fig. 144, *l.l.*, *l.s.*)

Thus as the animal grows it moves forward, building about it an ever enlarging shell and at certain intervals shutting off by a septum the empty shell, which it thus leaves behind, and maintaining connection with the empty portion only by the siphon which enters the successive chambers through apertures in the septa.

The unoccupied chambers are filled by a gas which resembles air but with a somewhat larger proportion of nitrogen. These gas-filled chambers seem to support the shell in the water to a sufficient extent to relieve the animal of its weight in swimming or floating.

The tubular prolongation of the mantle, *i.e.*, the siphon left behind in the apertures of the successive septa, secretes about itself a calcareous wall, the *siphuncle* (Fig. 139, *sl.*), just as the posterior portion of the mantle elsewhere has built the septum. That portion of the siphuncle, called the siphonal collar, which projects backwards a short distance from each septum, is built by the enlarged anterior end of the siphon where it joins the mantle at the body; it is heavier and hence more likely to be preserved fossil than the remainder of the siphuncle.

An external depression or opening, called the *umbilicus*, is visible at the center of the coils in *Nautilus umbilicatus;* in *N. pompilius* the outermost volution so envelops the inner ones that no opening is visible. The dark portion of the coil just inside the aperture is covered during life by a convex fold of the mantle extending upward from the umbilicus of the shell.

The body is held in the shell by strong **muscles** whose large crescentic areas of attachment are clearly visible on the inside of the living chamber near the umbilicus. The banded muscle scar connecting these two areas marks the place of attachment of three muscular (aponeurotic) bands which serve likewise in attaching the body to the shell and are called collectively the annular muscle or annulus (Fig. 139, *an.m.*).

The **body** when removed from the shell is found to be roughly oblong in outline and between six and seven inches in length. It is divided into a large, distinct head, bearing eyes and tentacles, and a rounded trunk. The ventral portion of the body is on the external or convex side of the shell, the dorsal on the inner or concave side.

The mouth is at the free extremity of the head region and is surrounded by slender tentacles, sixty in the male, ninety in the female; these are situated on the edges of a series of fleshy lobes which represent the anterior part of the foot of other mollusks. Each tentacle consists essentially of two parts, — a slender cirrus and an elongate, tubular sheath into which the cirrus can be retracted for protection.

The *tentacles* serve the double function of prehension and adhesion, being used for seizing food and for attachment to surfaces. They are provided with longitudinal, circular, oblique, and transverse muscles so that they are well equipped for a variety of muscular services. There are no true suckers as in the squid, but a kind of sucker-like efficiency is imparted to the tentacle by the contraction of certain of its muscles. Thus there are formed definite suctorial ridges on the lower and inner surfaces of the tentacles, and Nautilus can hold to the surface of attachment with considerable tenacity. The lower portions of the tentacles on the inner or dorsal side of the head are fused into a thick muscular lobe, the *hood*, which serves like the operculum of gastropods to close the aperture of the shell when the body is withdrawn into the living chamber. On the ventral side of the head region is the *funnel* or *hyponome* (Fig. 139, *f.*); this looks like a thick, muscular leaf with free, rolled-in edges. The position of this funnel is indicated on the exterior of the shell by the hyponomic sinus, a down-bending of the lines of growth on the ventral (outside) portion of the shell.

The short, rounded body is enveloped by the *mantle*, which is prolonged posteriorly into the fleshy, hollow tube of the siphon, extending backward within the siphuncle of the shell through all the otherwise empty chambers. Anteriorly the mantle is

produced into a free flap surrounding the head and attached to the shell near the edge. When the large mantle cavity is opened, there are seen the two pairs of gills, the two pairs of osphradia, and the sac-like body wall containing the viscera. Opening from this sac into the mantle cavity are the apertures for the discharge of the waste and reproductive products.

Water is admitted into the mantle cavity through the wide cleft between the free anterior edge of the mantle and the wall of the visceral sac. It bathes the gills and into it are thus discharged the effete products of respiration. It likewise receives the waste products discharged from the intestine and the products of the excretory and reproductive organs. After the admission of the water, the mantle cleft closes almost completely by appression of its walls, and contraction forces the water out through the funnel. The successive jets of water thus violently expelled through the funnel act as an oar in pushing the animal backward; this is its normal mode of locomotion.

Respiration is effected through the gills. These are two pairs of plume-shaped bodies attached to the wall of the mantle cavity and consist of delicate lamellæ with thin walls. The blood is carried throughout the gills in a system of minute branches and through their thin walls exchanges the waste gases it has collected from the body for the oxygen of the water which bathes the outside of the gills in the mantle cavity. It is then gathered up into vessels leading back to the auricle of the heart.

The **digestive canal** passes back in a straight line from the mouth, through the buccal cavity, œsophagus, and crop to the stomach at the posterior extremity of the visceral mass. From the stomach the intestine bends abruptly, develops a rounded cæcum, and proceeds in a nearly straight line to the anus, which opens into the mantle cavity. A very large digestive gland, the "liver," opens into the cæcum.

The *food* is largely small crustaceans, especially one species of decapod; the shells of these are easily crushed by the strong jaws. These and the small fishes, and mollusks which serve likewise for food, are seized by the tentacles and passed into

the mouth, where they are torn by the powerful movement of the jaws. The jaws form a sort of beak situated just inside the thick-walled buccal cavity. They are mainly composed of hard black chitin but are calcified on the biting edges. Experiments in baiting have shown that so sharp are the jaws and so powerful their closing muscles that Nautilus is able to cut off the leg of a chicken as if with a pair of shears. The upper jaw fits closely inside the lower so that their action in biting is like that of a steel shear where two heavy blades having sharp square corners move past each other. The jaws form the main part of the buccal mass, leaving a comparatively small buccal cavity. As in the Gastropoda, Scaphopoda, and Amphineura, the floor of the buccal cavity bears a *radula,* set with pointed teeth, also a large fleshy projection called the tongue. The walls of the intestine are extremely thin and have an abundant supply of blood vessels which thus are in position to gather up the products of digestion from the digestive canal and carry them throughout the body.

The *heart* consists of a large, muscular ventricle into which open four blood vessels, one from each of the four gills. The blood passes from the ventricle in five arteries, the divisions of which penetrate all parts of the body. These arteries finally subdivide into capillaries and from these the blood passes into the sinuses — extensive blood spaces in the various tissues.

Four nephridia or *kidneys* discharge their waste products into the mantle cavity. It is seen, then, that excretion of the body wastes is effected through the kidneys and gills which purify the blood, and by means of direct discharge by the anus through which passes the unused products of digestion.

The **nervous system** possesses no distinct ganglia, the central nervous system being represented by a very thick nerve collar surrounding the œsophagus. From this collar pass nerves to the various organs of the body.

Sense organs. — The *eyes* (Fig. 139, *e.*) are very large, nearly an inch in diameter, but extremely simple, each consisting essen-

tially of a saucer with convex bottom attached to the side of the head by a stalk and with the top covered by a disk perforated by a central aperture; this saucer is lined by the retina and possesses no lens or vitreous humor. It is filled by the sea water, which has free access through the aperture at the top. Thus the naked retina is bathed by sea water on one surface and receives the fibers of the optic nerve on the other.

It is considered probable from experiments in baiting Nautilus that the animal is guided in the capture of its prey largely by the generalized sense of taste and smell. (Though the eyes are doubtless likewise useful, still their simple character and the darkness of the depths where Nautilus is usually found would render them less useful guides.) Four modified tentacles, the so-called ocular tentacles, are supposed to serve this function. They differ from the other tentacles in the possession of vibratile cilia, and their sensitiveness is shown by their instant retraction when touched by a foreign body — a sensitiveness not shared by the other tentacles, whose function is mainly adhesive. (The Dibranchia do not possess these accessory tentacles, and it has been suggested that this difference is to be correlated with the fact that while Nautilus finds its food chiefly by this chemical sense, the Dibranchia find it chiefly by the aid of their remarkably perfect eyes.)

The organs of hearing or of balancing are the two *otocysts*, little sacs near the nerve collar, which are almost completely filled by a large number of otoliths, tiny crystals of calcium carbonate.

The four osphradia situated in the mantle cavity near the gills are probably also sense organs; they are knob-like projections containing nerve cells.

The **sexes** are separate, each individual possessing a single testis or ovary near the posterior end of the body. These discharge their products through ducts into the mantle cavity.

The eggs are laid singly, each egg being about an inch and a half long and surrounded by two thick shells.

The development of Nautilus is not yet known.

1. What is the present habitat of Nautilus? Its geologic range?

2. Sketch the shell of a living species of Nautilus (*a*) side view; (*b*) view looking into aperture; (*c*) cut portion of section parallel to plane of coiling. Label aperture, living chamber, septa, siphuncle, muscle scars.

3. How are the septa secreted? Give a probable theory as to the cause of their presence and equal spacing.

4. What was the function of the muscles which caused the scars upon the inside of the shell?

5. Describe the siphon; its relation to the siphuncle.

6. How does Nautilus creep? While creeping what is the position of the funnel? the coil of the shell? How does it differ in this respect from a gastropod like Helix?

7. What are the functions of the tentacles? What is the hood? its function?

8. Describe the hyponome; its function. How is its presence indicated upon the shell?

9. What portion of the body secretes the shell? the siphuncle?

10. What organs are located in the mantle cavity?

11. How does the animal breathe?

12. Name two modes of progression of the animal.

13. What is its food? How caught and eaten?

14. Briefly describe the circulation of the blood.

15. What waste products are there and how are these thrown out of the body?

16. What are the principal differences between the nervous systems of the cephalopod Nautilus and the gastropod Busycon?

17. Describe the eye of Nautilus; the otocyst.

18. Are the sexes united or separate?

19. What are sutures? Examine them upon a fossil Nautilus.

20. What is the direct cause of the coiling during the growth of the shell?

21. What part of the mantle secretes the "mother-of-pearl" of the shell? What is the cause of its brilliant luster?

22. Label on the sketch 2, (*c*) the dorsal and the ventral portions of the shell. How does it differ in this respect from gastropods, *e.g.*, Busycon and Helix?

General Survey of Class Cephalopoda

Cephalopods are bilaterally symmetrical mollusks, with the foot transformed into a crown of appendages surrounding the mouth and a funnel-shaped swimming organ, the hyponome.

The mouth is provided with jaws and a radula. The nervous system is highly developed. The sexes are separate.

In the cephalopods the primitive molluscan plan may be considered as modified by increase in the height of the body and reduction of its length. The foot has shifted forwards and becomes involved in the " head," its edges growing around the mouth.

A shell may be present or absent and when present may be external or internal, and modified into various forms. The general method of shell secretion in the mollusks is described under the Pelecypoda, pages 267–269, 273.

If oriented with the head and arms down, in the position assumed by Nautilus when moving over the sea-bottom, the visceral mass is on top as in the normal position of gastropods, but unlike gastropods is not twisted. The shell likewise differs in being coiled dorsally, *i.e.*, the outside of the curved shell of Nautilus is the ventral portion, of gastropods it is the dorsal. (Compare Figs. 137 and 140.)

Cephalopods are exclusively marine. They are preyed upon by whales, seals, and sea birds. It has been suggested that ambergris is composed largely of cephalopod tissue which has been voided by whales.

Derivation of name. — > Greek *cephale*, head, + *pous* (*pod*), foot. The foot of other mollusks is here transformed into the arms and funnel about the head.

Cephalopods are divided on the basis of the number of gills, into two orders:

1. Tetrabranchia.
2. Dibranchia.

Order 1. Tetrabranchia

Cephalopods possessing an external shell of many chambers, only the last of which is occupied by the body of the animal. Head region bearing many appendages with suckers, and saucer-shaped eyes open to the exterior and without lenses. Four gills and four kidneys present, but no ink sac.

Named in reference to the number of gills from Greek *tetra*, four, + *branchia*, gills.

This order is represented by but one living genus, Nautilus, which has flourished from Tertiary to present times. There are, however, a great many fossil cephalopods found in Paleozoic and Mesozoic rocks which, though not affording much information as regards the anatomy of the living animal, such as the number of gills and kidneys, are classed with this order because their shells agree closely with that of Nautilus.

Cephalopods have been competitors of the vertebrates in the oceans from Silurian time to the present. Sections through the living chambers of different Paleozoic species show scales or other armor of the fish then living, indicating that such animals formed part of their food.

This order includes the two great groups Nautiloidea and Ammonoidea; the former have a non-calcareous and the latter a large calcareous initial chamber, the *protoconch* (Fig. 143, *pr.*). The siphuncle in the nautiloids varies in position from dorsal to ventral, being often centrally placed; in ammonoids it is, with the exception of one group, ventral in position, *i.e.*, upon the outer edge of the coil. The curved growth lines of the hyponomic sinus almost invariably indicate the ventral side. In general the size of the siphuncle decreases from the nautiloids, through the ammonoids and belemnoids, to the sepioids, where it is a mere rudiment, distinguished with difficulty. This same relative decrease in the size of the siphuncle is seen in the development of an individual ammonoid from youth to maturity. Bactrites with its straight shell, simple sutures, ventral but submarginal siphuncle, peculiar collars, and large calcareous protoconch may be transitional between the two groups, the Nautiloidea and the Ammonoidea.

Suborder a. Nautiloidea

Shells straight, curved, or coiled. Sutures simple, *i.e.*, straight or undulated, never acutely angular. Living chamber usually with aperture notched by a hyponomic sinus for the

passage of the funnel. Siphuncle usually central or dorsal, *i.e.*, on inner margin of whorl, rarely ventral. Shells smooth or with simple ridges or nodes, never complexly ornamented.

Nautiloids are first known from the Cambrian rocks; they reach their maximum development in the Silurian and decline to the Triassic; since that period their retrogression has been slight. At present they are represented only by the genus Nautilus, which has given the name to the suborder.

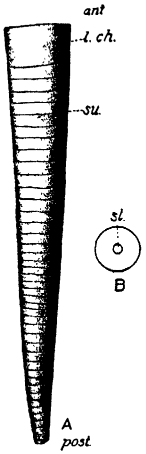


FIG. 141. — The cephalopod, *Orthoceras sociale* Hall, from the marine Maquoketa formation (Upper Ordovician) of Iowa. (× ½.) *A*, an almost complete internal mold of the shell showing the suture lines and probably most of the living chamber. *ant.*, anterior end; *l.ch.*, living chamber; *post.*, posterior end; *su.*, suture. *B*, an ideal cross section showing the siphuncle (*sl.*). (*A*, after Clarke.)

Orthoceras (Fig. 141). *Ordovician to Triassic.*

Shell usually straight, in the form of a long, tapering cone (whence the name from Greek *orthos*, straight, + *ceras*, a horn). Surface smooth. Living chamber long. Sutures simple, straight or nearly so. Siphuncle usually central.

1. Sketch (*a*) side view; (*b*) top view. Label sutures, living chamber if present, siphuncle.
2. How do you account for the succession of chambers and their equal spacing?
3. What was the function of the siphuncle?
4. What part of the body secreted the shell?
5. What chamber did the body occupy at the time of the animal's death? Was the siphuncle filled or empty during life?

Ryticeras (Fig. 142). *Devonian.*

Shell varying from slightly curved to loosely coiled. Siphuncle ventral, slightly expanded between the septa. Surface marked by coarse bands and at times by spinous processes.

1. Sketch side view, showing curve of shell.

Nautilus (Figs. 2 (left), 139, 140). *Tertiary to present.*

Four living species of Nautilus are known; these are from the Indian and Pacific Oceans. *N. pompilius* is described on page 303.

Suborder b. Ammonoidea

Shell usually closely coiled in a flat spiral. Sutures more or less complex, at times acutely angular. (Figs. 2 (right), 7, 144.) Siphuncle small, and situated near the ventral (outer) margin. Surface often highly ornamented with ridges and nodes.

In some ammonoids the aperture of the shell was closed, after the withdrawal of the animal, by a plate corresponding in function to the operculum of the gastropods, and probably secreted by such a muscular lobe as the hood of Nautilus.

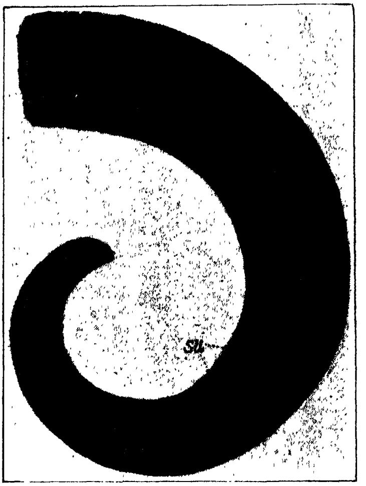


FIG. 142. — Internal mold of the shell *Ryticeras trivolve* Conrad, from the Onondaga (Middle Devonian) of New York. (× ⅘.) *su.*, sutures. (From Hall.)

Ammonites are especially important as index fossils in the Mesozoic. They are known from the Silurian to the Cretaceous inclusive.

As this suborder is wholly extinct, we are dependent for knowledge of the animal and its habits wholly upon the information afforded by the shell and the character of the rock in which it is found. It was probably closely comparable with Nautilus. A few were swimming forms as is indicated by the presence of a hyponomic sinus on the shell, the mark of the swimming organ — the hyponome; but most ammonites were apparently able only to crawl. The apertures of these latter have in place of the hyponomic sinus a pointed prolongation of the ventral portion of the shell, the rostrum.

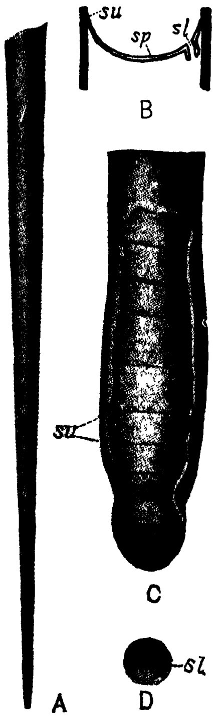


FIG. 143. — *Bactrites gracilior* Clarke, from the Naples beds (Upper Devonian) of New York. *A*, a nearly entire shell (× ¾). *B*, an ideal longitudinal section showing septum (*sp.*), suture (*su.*), and siphuncle (*sl.*). *C* (× 20), apex of shell showing protoconch (*pr.*) and, where the shell is broken away, the sutures (*su.*). *D*, upper surface of a septum showing siphuncle (*sl.*). (After Clarke.)

Bactrites (Fig. 143).

Devonian to Pennsylvanian.

Shell straight, gradually tapering, round or compressed elliptical in section (whence the name, from Greek *bactron*, a staff, + *ites*, meaning stone). Sutures simple except for the small ventral lobe. Siphuncle ventral, sub-marginal.

1. Sketch (*a*) side view showing ventral lobe; (*b*) top view; label sutures, ventral lobe, siphuncle.
2. Why is this not included with the sub-order Nautiloidea?

Muensteroceras (Fig. 144).

Mississippian.

Shell coiled into a thick disk. Umbilicus moderately wide, with angular margin. Sutures with angular lateral lobe and broad lateral saddle, and with a narrow lobe on the venter broken by a small notched saddle.

All shells with the above type of simply angular sutures were formerly classed as *goniatites* (from Greek *gona*, a knee).

1. Sketch view showing coils, noting sutures, lobes, saddles, umbilicus; indicate the ventral side.
2. How was the umbilicus formed?
3. Sketch an entire suture from venter to umbilicus.
4. What is a suture?
5. What determines the dorsal and ventral sides of a shell?

Placenticeras (Fig. 145).

Upper Cretaceous.

Shell coiled into a thin disk. Suture

complex, made up of numerous serrated lobes and saddles (the *ammonitic* type of suture); the third lateral lobe is the deepest, after which there is an abrupt decrease.

1. Sketch (*a*) circular view of specimen showing sutures; (*b*) view showing aperture.
2. What is the relation between septum and suture?
3. Under what conditions do sutures become visible?

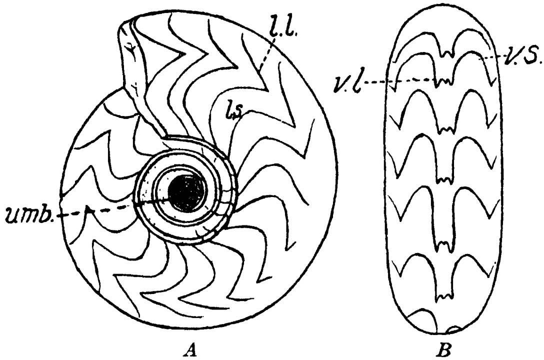


FIG. 144. — An ammonite, *Muensteroceras oweni* Hall, abounding in the ocean covering Indiana during Kinderhook (Lower Mississippian) time. Natural size. *A*, side view. *B*, ventral view. Sutures *goniatitic; l.l.*, lateral lobe; *l.s.*, lateral saddle; *umb.*, umbilicus; *v.l.*, ventral lobe; *v.s.*, ventral saddle. (Redrawn from Hall.)

Scaphites (Fig. 146). *Upper Cretaceous.*

Coiled in a plane spiral with the whorls in contact and embracing, except the last, which often becomes somewhat uncoiled and detached from the spiral and recurved in the form of a hook. Surface ornamented with bifurcating ribs which often bear tubercles; ribs continuous across the venter. Sutures generally much divided with several auxiliary lobes. Name from Greek *scaphe*, a boat, + *ites*, meaning stone, in reference to the shape.

The variety *S. nodosus brevis* is exceedingly abundant in the Upper Cretaceous of the Rocky Mountain region, also in New Jersey.

1. Sketch (*a*) view of spiral; (*b*) apertural view; (*c*) interior of section of entire shell cut parallel to the plane of coiling; note siphuncle, sutures, ribs, septa.

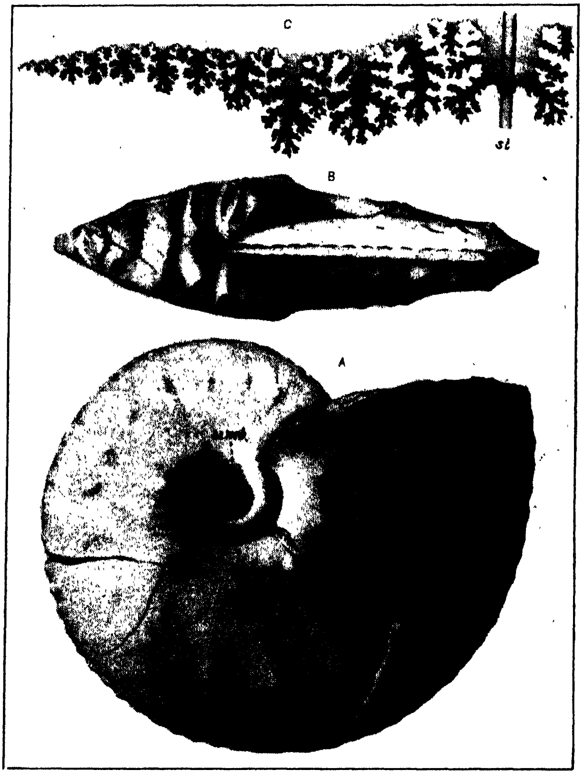


FIG. 145. — The ammonite, *Placenticeras intercalare* Meek, from the Pierre formation (Upper Cretaceous) of South Dakota. *A*, side view of specimen (× ½). *B*, apertural view. *C*, suture of same from siphuncle (upon the outer edge of the coil) to umbilicus (*umb.*). *sl.*, siphuncle. (From Meek.)

2. How much of the entire shell did the body of the animal occupy during life? Compare with gastropods.

3. On shell 1, (*c*) follow a septum from its center to its outer edges, — the sutures; note it gradually changing from the simple, flat septum into the very complex lobes and saddles of the sutures. (A section of

any ammonoid shell will show the same change.) Compare this with a similar section through a fossil Nautilus; what difference do you note?

4. What principally distinguishes the Ammonoidea from the Nautiloidea?

5. Distinguish the ammonitic type of suture from the goniatitic; give examples of each.

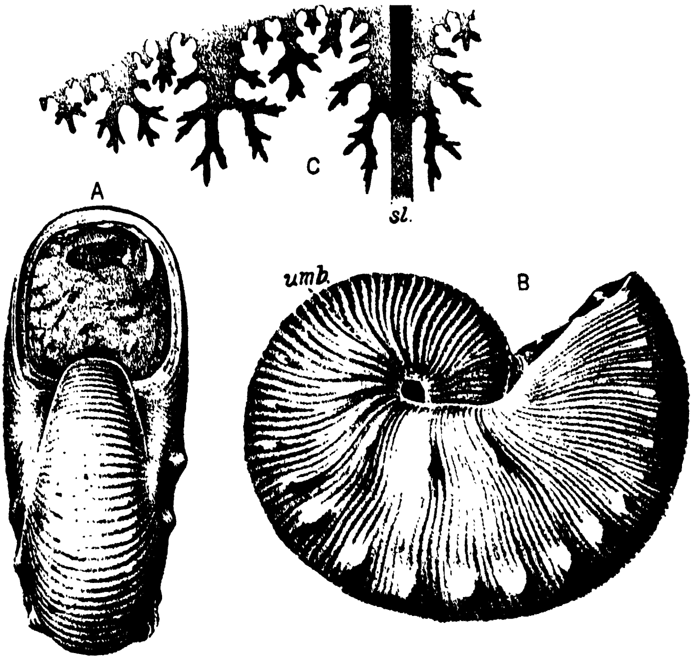


FIG. 146. — *Scaphites nodosus*, var. *brevis* Meek. An entire shell from the Pierre (Upper Cretaceous) of Montana. *A*, view of opening of living chamber (× $\frac{3}{4}$). *B*, side view. *C*, the suture (× $1\frac{1}{2}$) extending from the position of the siphuncle (upon the outer edge of the coil) to the umbilicus (*umb.*). *sl.*, siphuncle. (From Meek.)

Baculites (Fig. 147). *Upper Cretaceous.*

Straight (except the first-formed part, which is spiral), elliptical in section. Sutures with the lobes symmetrically divided. Named from its shape, from Latin *baculum*, a staff, + *ites*, meaning stone.

B. compressus is abundant, associated both east and west with the variety of Scaphites noted above and with several species of the pelecypod Inoceramus.

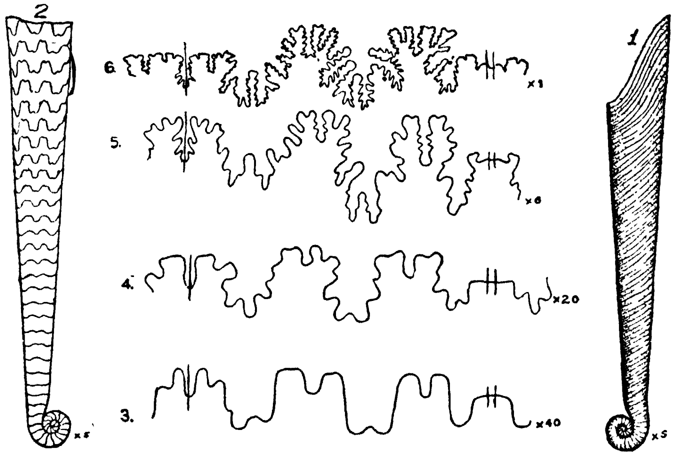


FIG. 147. — *Baculites compressus* Say, from the Upper Cretaceous of South Dakota. 1, a young shell preserving the early coils. The living chamber occupied about one half the length of the shell. 2, a specimen of same size as the last but with the outer shell broken away revealing the sutures, — the outer edges of the septa. Note the variation in the sutures from the apex of shell 2 to its wide end and on through the progressively larger shells as shown in 3, 4, 5, and 6. 6 represents the condition of the suture in the adult shell. (After Brown.)

1. Sketch (*a*) the elongate flattened surface of a specimen showing the sutures; (*b*) top view; label sutures, lobes, saddles, umbilicus, septum, siphuncle.
2. These fossils usually occur with mud filling all the chambers. How did the mud penetrate the chambers?
3. Distinguish between septa and sutures.
4. What does a single perfect shell of Baculites suggest as to its ancestry?

Order 2. Dibranchia

Cephalopods with shell internal or wanting, or exceptionally external but not chambered (Argonauta). Head bearing eight or ten arms around the mouth; these are furnished with suckers.

The eyes are very large and of complex structure. Two gills and two kidneys are present. An ink sac discharges its contents through the funnel when the animal is startled, thus constituting a means of defense, since under cover of the blackened water the animal may escape. Indications of this ink bag are often present in fossil forms in the shape of an external mold of the sac, and even in carbon particles, the remains of the ink itself.

The life of the Dibranchia is more active than that of the Tetrabranchia and there follow certain modifications, especially in the mantle. This in the majority of mollusks has a merely passive function to protect the viscera and secrete the shell. In the Dibranchia there is no external shell, and the mantle becomes thickened and highly muscular; its expansion and contraction cause a powerful current of water to be drawn into the mantle cavity and expelled through the tubular funnel. The animal is thus enabled to swim rapidly and to float. The aggressive manner of life thus fostered by these modifications is aided by the development of suckers on the appendages about the mouth and by the special modification (in the suborder Decapoda) of two of the arms for the capture of prey (Fig. 148).

The typical internal shell is seen in Belemnites, a fossil form described below. The shell is absent in the devil-fish (Octopus).

The Dibranchia are known from the Triassic to the present.

Ommastrephes (Fig. 148). *Living.*

This marine, free-swimming animal is world-wide in its distribution. In general all forms similar to this genus are commonly called *squids*. It has a distinct head bearing ten long, very muscular arms and two large, highly developed eyes; two of the arms are much larger than the other eight. The head is separated from the trunk by a constricted region, the neck. The trunk is elongate, shield-shaped, bordered laterally by a fleshy fin. The entire body is surrounded by a thick muscular mantle which is free from the body except along the median dorsal line.

The *skeleton* is entirely internal; it consists principally of the narrow pen of conchiolin (Fig. 148 *D*, *E*) passing the entire length of the trunk and protecting the visceral organs dorsally. There are, in addition, several somewhat horny cartilages which are supporting and protective in function. The cranial cartilage protects the principal nerve centers and supports the eyes; other cartilages support the bases of the fins and the arm bases.

Another protective organ is the *ink sac*. This is located in the posterior part of the trunk and secretes a dark brown substance. When the squid is startled, it discharges this fluid through the duct opening within the anus, where, mixing with the water in the mantle cavity, it is discharged through the funnel as a black cloud under cover of which the animal escapes. Squids travel in schools which often include thousands of individuals.

Locomotion. — The squid can dart with great rapidity, partly by the arms, partly by the muscular, lateral fins, but principally by the rhythmical contraction of the mantle. The expansion of the mantle draws water through the slit between the anterior edge of the mantle and the body into the mantle cavity. Muscles then close this opening and the contraction of the mantle forces the water out through the funnel, causing the animal to move in the opposite direction. It can move in any direction by simply bending the funnel in the direction opposite to that in which it wishes to move. A valve prevents the water from entering the mantle cavity through the funnel.

The animal's *food* consists of mollusks, crustaceans, and fishes which it catches with its arms. The arms are furnished on the inside with many suckers.

Each *sucker* is a shallow cup supported on a short stalk; its membranous lip is lined internally by a narrow, horny rim and in the middle of the bottom of the cup is a piston-like plug which, when drawn down by the contraction of muscles, produces, when held against a solid object, a partial vacuum and resulting adhesion. The prey stands little chance of escape when surrounded by arms lined by hundreds of such suckers.

The *eyes* are much more perfect than those of Nautilus, and are next in order of development to those of the vertebrate.

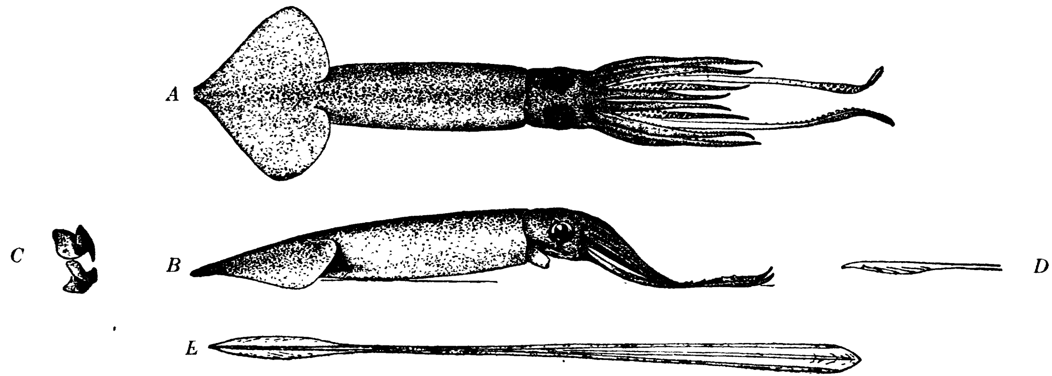


Fig. 148. — An American squid, *Ommastrephes illecebrosa* Les. ($\times \frac{1}{4}$), from the Atlantic Ocean at Provincetown, Mass. *A*, dorsal view. *B*, side view of animal asleep; note how the water for respiration is kept pure by the elevation of the anterior mantle slit above the mud. *C*, the jaws in position. *D*, side view of tip of skeleton. *E*, upper view of entire skeleton. (All drawn from life by J. Henry Blake.)

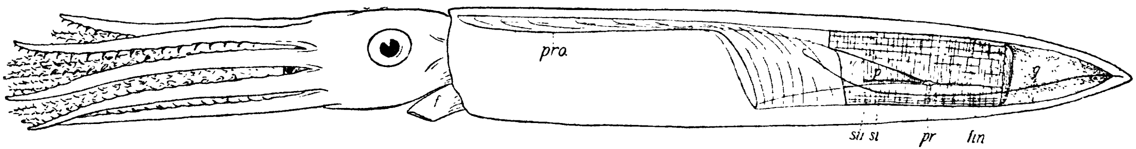


Fig. 149. — A restoration of *Belemnites*. The guard is that of *B. densus* of the Jurassic of Wyoming. ($\times \frac{1}{2}$.) *f*, funnel; *g*, guard, its upper portion sectioned vertically to show the phragmocone; *p*, phragmocone; *pr*., protoconch; *pro*., proöstracum; *si*., siphuncle; *su*., suture of the phragmocone dividing it into chambers.

Light rays passing through the protective transparent cornea are bent towards the pupil by the water filling the external chamber of the eye; this chamber is open by a small hole to the sea water. The pupil is an opening through the firm wall of the eye; the portion of this wall immediately bounding the pupil and called the iris contains muscle fibers by whose action the pupil can, to a limited extent, be enlarged or diminished. The light is then focused upon the retina by passing through the spherical, dense lens and next through the large mass of jelly-like vitreous humor.

There are two *otocysts* in the posterior portion of the head; these have the power of coördinating movements in maintaining equilibrium, and are possibly also functional in hearing. There may also be present a sense of smell and of taste.

The *sexes* are distinct. The eggs are fertilized through copulation.

Belemnites (Fig. 149). *Jurassic to Cretaceous.*

Belemnites is closely related to the squid. Impressions of the tentacles and arms are sometimes found preserved in the fossil state, showing the suckers provided with horny hooks. The mandibles and ink sac are likewise at times found with the ink preserved in the form of solid carbon particles. The shell, however, is more complete than that of the squid, consisting of three parts — guard, phragmocone, and proöstracum. The *guard* is solid, and when examined in section is seen to be composed of prisms of calcite radiating from an axial line slightly nearer the ventral surface. The *phragmocone* fits into the hollowed end of the guard, the *alveolus*, and is divided into chambers by septa which are perforated by the ventrally placed siphuncle; this is followed by the calcified, blade-like *proöstracum.* The proöstracum corresponds to the pen of the squid and probably in life afforded dorsal protection to the viscera. The phragmocone corresponds to the entire shell of the Tetrabranchia.

As an index fossil of the Jurassic and Cretaceous Belemnites is scarcely less important than the ammonites. The name, from the Greek *belemnos*, a dart, was given by Agricola in 1546. It is commonly called "arrowhead" or "finger stone" from the

shape, and "thunderbolt" or "thunder stone" from its supposed origin.

1. Split the broad end of a specimen longitudinally from the ventral groove backwards (if the narrower end splits likewise, this should be glued into place again). Sketch view showing this section. Label alveolus, guard.

2. Note the calcareous, prismatic fibers of which the guard is composed, and the successive conical layers by means of which the guard increases in size. Make a cross section showing this increase.

3. The walls of the alveolus usually show faint impressions of the chambered phragmocone, the siphuncle of which was located ventrally, *i.e.*, upon the side next the ventral groove. Indicate upon the first sketch the ventral and dorsal sides.

4. What is the significance of the name Belemnites?

In the genus **Sepia** (Tertiary to present) the shell is likewise internal but extends the entire length and breadth of the body. It is without differentiated phragmocone and guard, but consists essentially of proöstracum or "pen." The projecting point may represent the guard. This is the familiar cuttle bone of commerce. *Sepia officinalis* is very common in the Mediterranean. The coloring matter from its ink sac is insoluble in water and gives a beautiful brown color much used in monochrome drawing.

Other living genera of the Dibranchia are the devil-fish (Octopus) and the Argonaut. Common American squids are Loligo and Ommastrephes.

Evolution of the Mollusca

The mollusks probably evolved from some primitive annelid group; both phyla pass through a trochosphere larval stage. In all mollusks except the scaphopods, the mantle exhibits a frequent tendency in the more active forms to grow around the shell. Since in these the shell has lost its protective character and is only an added weight and causes a useless expenditure of energy, it gradually atrophies. The primitive molluscan shell, at least in the gastropods and cephalopods, was apparently

cap-like, something like the modern limpet. In the former the body elongated with the downward growth of the shell and it thus continued to occupy the entire shell. In the cephalopods the body remained compact and thus the downward growth of the shell was accompanied by the withdrawal of the body at intervals from the earlier portion of the shell, secreting at each resting place a septum. Since a long straight shell is unmanageable, natural selection caused the survival of those tending towards a coiled condition.

The Amphineura represent that branch of the mollusks which secreted a protective skeleton of separate spicules or one of eight dorsal plates. In the pelecypods two plates were secreted, in all the others only one.

Of the five distinct radiations, only two sent offshoots into fresh water. The pelecypods in the early Paleozoic were all normal marine forms. Fresh-water shells are first known from the Devonian. None have taken to a distinctly land habitat, though a few to-day may exist for some time in the midst of wet moss. This is probably due to the animal being dependent for food on water-borne particles. The gastropods of the early Paleozoic were also marine. In the Devonian, a few brackish water forms (Siphonariidæ) appeared and in the Carboniferous some land snails (Pupidæ, etc.), and both habitats have continued to be occupied to the present. The first fossil fresh-water snails are from the late Jurassic. It is difficult to understand why the cephalopods have not sent forth branches into the fresh waters, but they are physiologically intolerant of even brackish water.

The gastropods as a class show to-day much more organic energy than do the pelecypods. Both the pelecypods and scaphopods have specialized to a life buried in mud or sand, the gastropods and cephalopods to a greater freedom of movement.

Among the cephalopods the nautiloids appeared first with their simple sutures. Probably from these the ammonoids evolved in the mid-Paleozoic; in these the sutures became more

and more complex until their disappearance at the close of the Mesozoic. Probably from some ammonoid stock of the late Paleozoic, with a tendency to more active swimming habits, arose the squids and their kin. In these there occurred an overgrowth of the shell by the mantle and the formation around the shell of a secondary calcareous sheath (the guard). This is prolonged on one side towards the head of the animal into the proöstracum. The guard becomes longer than the chambered shell (called here phragmocone). In Aulacoceras of the Triassic, the phragmocone is still very long, fully two-thirds the length of the guard and easily detached, in which state it is usually found fossil. Different directions of evolution are noted in these internal skeletons. In our common squid, Ommastrephes, there is a loss of the phragmocone and guard, retaining only the proöstracum. In the modern Sepia (cuttle-fish) derived through Belosepia of the Eocene, the septa of the phragmocone are extended as close-set layers up the surface of the proöstracum. In Spirula, derived through Spirulirostra of the Miocene, only the phragmocone persists and this is partly external.

Mollusks as Rock-Builders

The mollusks are important agents in the formation of limestone from the early Paleozoic to the present. Just as mollusk coquina is being formed to-day in many warm seas, as on the coasts of Florida (Fig. 150), so it was formed frequently throughout earth history. Pelecypods are the most important class in this respect, especially since the beginning of the Mesozoic when the more prolific and the heavier-shelled genera came into existence. During the Cretaceous especially, many of these occurred gregariously in large numbers, forming bedded limestone reefs. Ostrea, Chama, Inoceramus, Exogyra, and the rudistids (Radiolites, Hippurites, etc.) are especially noteworthy. In the Texas region of North America may be mentioned the Gryphæa beds of the Fredericksburg, the Ostrea beds of the Eagle Ford, the Exogyra beds of the Taylor marl, and the *Exogyra arietina* beds of the Del Rio formation (Figs. 124, 151). Ino-

ceramus is exceedingly abundant at various horizons throughout the Upper Cretaceous of the Rocky Mountain and Great Plains area.

Next in importance were the cephalopods. During the Paleozoic the nautiloids added considerably to the formation of strata. The ammonites that lived in all the Mesozoic oceans were most important in this respect. The Triassic limestone formed in

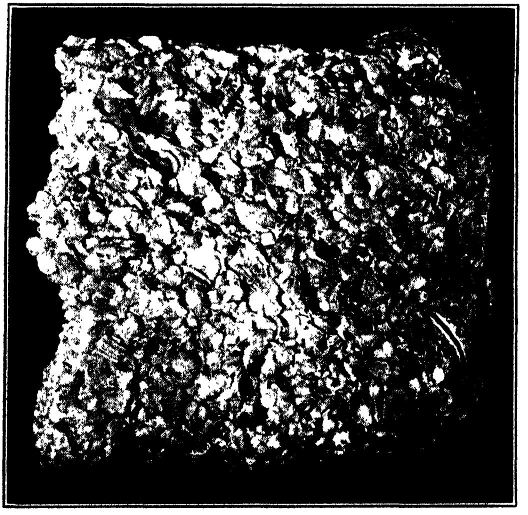


FIG. 150. — Recent coquina formed of pelecypod and gastropod fragments on the coast of Florida. These fragments show the subjection of the shells to the action of waves.

the old Tethys sea is crowded with them. They continue to be very important contributors throughout the Jurassic and Cretaceous. The belemnites are also of considerable importance during the Jurassic and Cretaceous. Strata of those ages are thickly strewn with their cigar-shaped internal skeletons.

Gastropods are important locally in strata ranging from the Ordovician to the present. Especially to be noted are the Bellerophon beds of the Tethys Permian of Europe, and to a less

degree, of the Rocky mountains. The *Turritella mortoni* beds contribute to the Eocene of Virginia. In the conularid group, Tentaculites (Fig. 136) is very abundant in the Silurian and Devonian, the strata being at times mainly composed of these fossil forms. Pteropods form up to 50 per cent of the mass of some present-day calcareous oozes in tropical and subtropical regions,

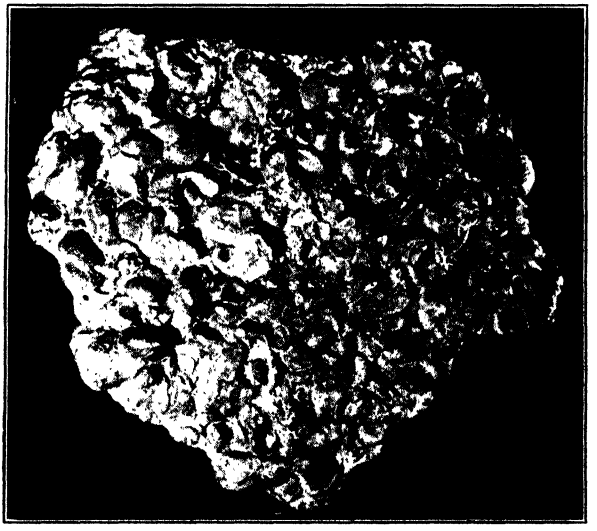


FIG. 151. — The "ramshorn" oyster, *Exogyra arietina*, which formed reefs upon the ocean floor in Texas during Lower Cretaceous time.

such as east of the Antilles and around the Fiji Islands. In the Devonian of western New York, *Styliolina fissurella* forms a limestone stratum from six inches to a few feet in thickness and with a horizontal extent of 60 miles; 40,000 individual shells occur in a cubic inch.

Amphineurans, although present since the Ordovician, have never been abundant.

1. Divide the phylum Mollusca into classes and all minor subdivisions, giving example of each.
2. What characters are common to all the Mollusca?

3. In what respects do mollusks show an advance over preceding phyla?
4. Describe the mantle in the various classes.
5. What is the structure of the shell? How is it formed? Explain the origin of ribs, spines, pearls.
6. Briefly outline the evolution of the Mollusca.
7. Discuss mollusks as rock-builders.

CHAPTER XIII

PHYLUM XII. ARTHROPODA

The Arthropoda are transversely segmented animals with mouth and anus at opposite ends of an elongate body, with muscles attached to the inside of an external skeleton (the very opposite of the vertebrates), and with a nervous system composed of a dorsal brain above the œsophagus, connected by nerves around this with a double ventral chain of segmentally arranged ganglia. A few or most of the body segments bear paired appendages, the distinct segments of which are separated by joints and moved by special muscles. Thus, as the animal does not need the movement of the skin for locomotion (as in the annulate worms) the skin secretes a horn-like substance, chitin, to form a hard outside skeleton. Since this rigid exoskeleton prevents increase in size, growth can occur only through the shedding or molting of this chitin. Eyes are nearly always present and are simple or compound. The cavity of the body between the exoskeleton and the internal organs consists largely of spaces, the blood sinuses, which are in full communication with the blood circulatory system. The heart, usually present, is elongate and is situated in a blood sinus from which the blood enters by valvular openings (ostia).

Derivation of name. — Greek *arthron*, joint, + *pous* (*pod*), foot, referring to the division of limbs into movable segments.

The phylum is subdivided as follows:

SUBPHYLUM 1. BRANCHIATA

Mostly water breathers; breathe by gills (branchiæ).

SUBPHYLUM 2. TRACHEATA

(except many of Class D)

Air breathers; breathe mostly by tracheæ.

CLASS A. CRUSTACEA

Type of the class, *Cambarus* (Fig. 152).

The crayfish, Cambarus, lives in fresh-water lakes, rivers, and pools, and is found in North America east of the Rockies and in eastern Asia. The only other genus of crayfish living in the northern hemisphere is Astacus; it is found in North America west of the Rockies, in Europe, and in western Asia. There are also some blind crayfish of the genus Cambarus inhabiting the caves in Carniola, southern Austria, which point to the former more extended occupation of Europe likewise by this genus.

The **body** is divided externally into the anterior unjointed portion, the cephalothorax (union of head and thorax) covered with the carapace, and the posterior portion, the abdomen, made up of distinct segments and terminating in the large horizontally flattened telson. The cephalothorax bears the eyes, feelers, and the five large walking legs. This division into head, thorax, and abdomen is not equivalent to the like division of the vertebrate body.

The body consists of twenty *segments* bearing upon their under side nineteen pairs of *appendages*. As can be seen by the appendages on the ventral side, the head consists of five segments bearing pairs of antennæ or feelers, the short and the long, one of mandibles or jaws, and two of maxillæ. The thorax is made up of eight segments bearing five large posterior or walking legs and three smaller anterior pairs or foot-jaws, with their bases toothed for passing the food obtained by them forward to the mouth. The abdomen consists of seven segments,

each of which except the last, or telson, bears a pair of appendages. In the female the five anterior pairs are small swimming feet or pleopods, while the sixth pair is much enlarged, each consisting of two flattened parts which with the telson compose the five-parted tail-fin, the principal organ of locomotion. The male differs only in having the anterior two pairs of pleopods converted into incomplete tubes for transferring the spermatozoa to the body of the female.

The *typical appendage* consists of one or more basal joints, the protopodite, which divides into two branches: an inner and ventral, the endopodite, and the outer and dorsal, the exopodite; this latter division is largely respiratory in function.

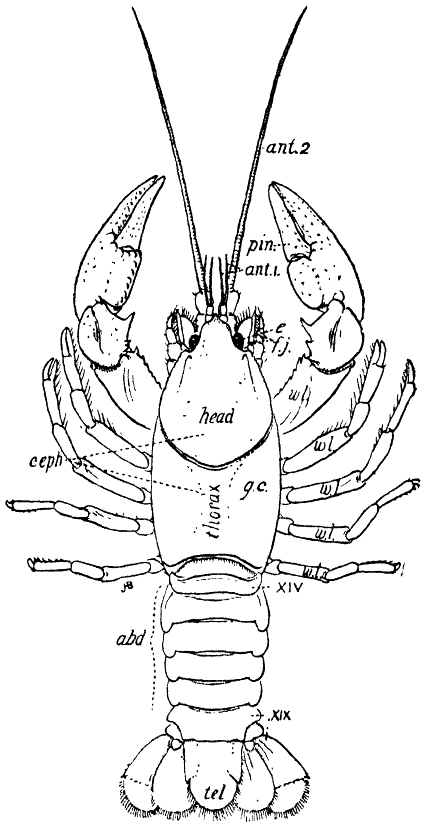


FIG. 152. — The crayfish, *Cambarus bartoni* Fabr. ($\times \frac{3}{4}$), from Colchester, Vermont. Dorsal view; *abd.*, abdomen; *ant. 1*, anterior antennæ; *ant. 2*, posterior antennæ; *ceph.*, cephalothorax; *e*, eye; *f.j.*, foot jaws; *g.c.*, gill-cover; *pin.*, movable arm of pincer; *tel.*, telson; *w.l.*, walking legs (five pairs); *XIV*, fourteenth body segment or first abdominal segment; *XIX*, nineteenth body segment.

The **skeleton** is external and is both protective and supporting to the muscles and other soft parts within. It is composed of chitin secreted by the epidermis, and hardened with more or less lime carbonate. It is segmented because it is thickened with lime carbonate in those regions not subject to bending, but remains thin and hinge-like in the intermediate spaces.

The *carapace* arises as a fold of the skin from the

posterior margin of the head region; dorsally it coalesces with the body segments, but at the sides it is free, forming the gill-covers (Fig. 152, *g.c.*). As these covers are unattached below, they permit the free entrance of water to the gills within, which lie between the sides of the carapace and the walls of the thorax proper.

Since the soft parts of the body are completely incased in resistant chitin, growth can take place only by a process of *molting* — of shedding the chitinous covering periodically (see Fig. 153). This is thrown off as a distinct whole. Not only is every part of the exterior shed, but also the lining of the œsophagus, stomach, and all of the intestine except the middle portion, though some internally shed chitin, however, as that of the stomach, does not leave the stomach, but is redigested. This molt, an exact copy of the exterior of the living animal, is shed about once a year during adult life, but oftener during the rapid growth of youth.

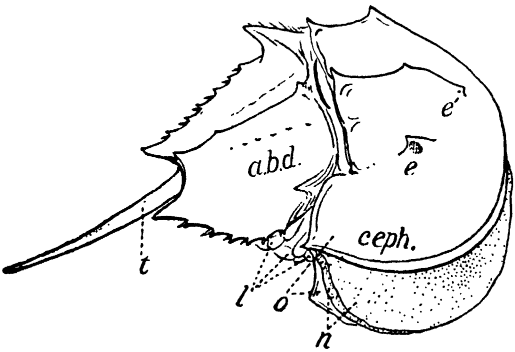


FIG. 153. — A young horseshoe crab, *Limulus polyphemus*, from the Massachusetts coast, molting. *abd.*, abdomen; *ceph.*, cephalothorax; *e*, a compound eye; *e′*, a simple eye; *l*, legs; *n*, newly molted portion; *o*, the edges of the old shell; *t*, telson.

The process of molting has been described as follows, a description holding true in general for all Crustacea: " Previous to the throwing off of the old skin a new soft one is formed inside " (the epidermis secretes new layers of chitin), " the lime is absorbed from the old shell in a dorsal line along the carapace, reaching from the rostrum to its posterior margin. Absorption also takes place at the joints of the limbs. The carapace now

splits along this dorsal median line of absorption, the blood leaves the limbs, which are thus made flabbier, and by involuntary muscular movements they are drawn, large claw and all, through the joints of the old shell. The anterior portion of the body is first drawn out through the dorsal vent, and lastly the tail. By means of the return of the blood to the limbs and the rapid absorption of water, the body . . . soon swells to a size far beyond that of the old shell." The lime taken up by the blood by absorption previous to molting is used in hardening the new shell, doubtless aided by the lime carbonate from pieces of shells, sea urchin spines, discarded lining of the stomach, etc., such have been found in the stomachs of crayfish and other Crustacea.

Beneath the epidermis is a layer of connective tissue, the dermis, to which the **muscles** are attached. They are thus fastened to and supported by the external skeleton. The muscular system consists principally of two longitudinal pairs of muscles, a large and complex ventral pair and a smaller simple dorsal pair, both extending the entire length of the abdomen and into the thorax from whose walls they arise. The dorsal pair or extensor muscles straighten the abdomen, while a portion (the flexor muscles) of the ventral pair bends it downward; the quick contraction of these latter powerful muscles causes the crayfish to dart rapidly backwards. It moves forward by the action of the abdominal swimming feet.

Of the five pairs of long thoracic legs, the four posterior ones are used in walking, the large anterior one with its huge terminal pincer for defense and offense. Each tube-like section of one of these is united to its fellow by a hinge-joint, hence movement can occur in but one plane, as at the knee and elbow in man; but since the axis of the hinge is different at successive joints, each entire leg can move in all directions. Movement is effected by an extensor and a flexor muscle fastened to the sides of each tube-like section and inserted in the sides of the proximal end of the next outer section; the movable arm of the pincer is similarly worked.

Digestive system. — The *food* of the crayfish is varied; it may be animal or plant, living or dead, but is largely decaying

animal matter. On account of their need of lime they are fond of stonewort (Chara). The smaller particles of food caught by the toothed bases (gnathobases) of the three anterior pairs of thoracic feet are carried forward by them to the mouth, as are the larger pieces caught by the huge claws. There the food is torn into bits by the toothed edges of the strongly calcified mandibles situated at its sides. Anteriorly the mouth is bounded by a single plate — the upper lip (labrum or *hypostome*); posteriorly by a pair of delicate lobes — the lower lip. The food passes from the mouth through the œsophagus to the gastric mill, a division of the stomach; this is lined with chitin and has three calcified teeth projecting into it from its walls (see Fig. 154). The mill is so moved by two pairs of muscles extending from it to the thoracic skeleton that the three teeth meet in the middle and thus complete the comminution of food begun by the mandibles. The food then passes to the smaller or pyloric division of the stomach; the numerous hairs which extend across this division act as a sieve to prevent all but the very fine food from passing on into the intestine. The stomach is thus merely a masticating and straining apparatus; digestion takes place in the small intestine. Into this is poured from the single pair of digestive glands a yellow fluid which digests both the proteids and fats, combining thus the function of both pancreas and liver of the vertebrates. The undigested remnant passes out through the large intestine and finally through the anus, which is situated on the ventral surface of the telson. With the exception of the sharp downward bending to the mouth the digestive canal is a straight tube extending the length of the body.

Since the œsophagus and stomach as well as the large intestine are formed by the inbending of the surface of the gastrula, they originate from the ectoderm as does the surface layer (epidermis) of the mature animals; hence they similarly secrete a lining of chitin which must be shed with each molt. Only the small intestine and its digestive glands are formed from the inner cell layer, the endoderm, of the gastrula stage.

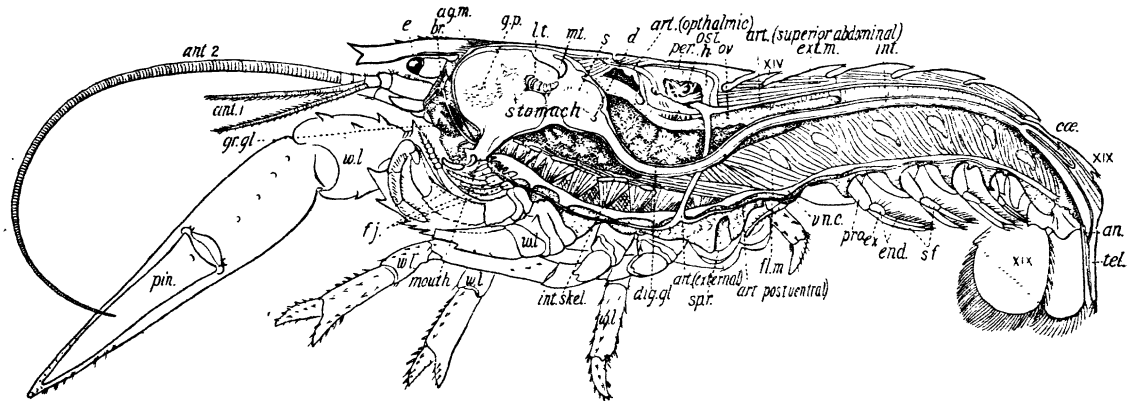


FIG. 154. — The American lobster, *Homarus americanus*, sectioned in the medium plane to show the internal anatomy and the relation of the external shell to the internal muscles and organs. (This section is essentially similar to that of the crayfish.) Reduced in size. *a.g.m.*, anterior gastric muscle; *an.*, anus; *ant. 1*, anterior antennæ; *ant. 2*, posterior antennæ; *art.*, artery; *br.*, brain; *cæ.*, cæcum; *d*, opening of duct of digestive gland; *dig.gl.*, digestive gland; *e*, eye; *end.*, endopodite; *ex.*, exopodite; *ext.m.*, extensor muscle, to straighten abdomen; *f.j.*, foot jaws (three pairs); *fl.m.*, flexor muscles, to bend abdomen; *g.p.*, gastrolithic plate, to secrete the stomach stones; *gr.gl.*, green gland or kidney; *h*, heart; *int.*, intestine; *int.skel.*, internal skeleton; *l.t.*, lateral tooth, and *m.t.*, median tooth of gastric mill; *ost.*, ostium, admitting blood from pericardium into heart; *ov.*, ovary; *per.*, pericardial sinus, — the sac inclosing the heart; *pin.*, movable arm of pincer; *pro.*, protopodite; *s*, sieve; *s.f.*, swimming feet; *sp.r.*, sperm receptacle; *tel.*, telson; *v.n.c.*, ventral nerve cord; *w.l.*, walking legs (five pairs); *XIV*, fourteenth body segment or first abdominal segment; *XIX*, nineteenth body segment. (Redrawn from Herrick.)

The absorption of the digested food takes place through the walls of the small intestine and its digestive glands directly into the blood (since the intestine is surrounded by a blood sinus) and thus finally into the heart.

The **blood circulatory system** consists of a muscular heart in the dorsal part of the thorax, arteries, capillaries, blood sinuses (cavities without definite walls among the muscles and viscera), and veins.

The rhythmical contraction of the heart forces the blood into seven arteries, which, dividing, extend into all parts of the body and finally into microscopic capillaries which terminate by open mouths in the blood sinuses. All blood sinuses communicate with the ventral sinus which runs the entire length of the abdomen and thorax, and conducts the blood to the veins on the gills. From the gills, veins carry it to the sac-like cavity (pericardial sinus) in which the heart is located. The blood enters the heart, upon the latter's rhythmical expansion, through three pairs of apertures with inwardly opening valves. The blood is a colorless fluid and all the corpuscles are similarly colorless (*i.e.*, leucocytes). When combined with oxygen it is bluish gray owing to the hæmocyanin in the fluid (not in the corpuscles), which like hemoglobin in mammals has great affinity for oxygen; it thus acts as the oxygen carrier from the gills to the tissues.

Respiration is performed by the gills, aided probably by the inner surface of the gill covers which bound them externally. Internally they are bounded by the wall of the thorax, since they are outpushings of the body wall. They are freely open below for the entrance of water. The renewal of fresh water is brought about by the vibratory movements of the exopodite of the maxilla, causing a current to set in over the gills from below and out in front.

The gills thus **excrete** carbon dioxide. Another excretory organ is situated at the base of each posterior antenna; this is the green gland which collects the uric acid, etc., in a urinary sac and discharges it through a duct opening on the proximal segment of the antenna.

The **nervous system** consists primarily of a brain in the dorsal region of the head united by nerve cords around the œsophagus

to the anterior end of a ventral nerve cord. The former supplies the eye, antennæ, etc. The latter is composed primarily of a double, ladder-like chain of ganglia united by connectives and extending to the posterior end of the body. Most segments have their own ganglia.

The **sense organs** include those of touch, sight, and possibly also smell and hearing.

The setæ on the two pairs of antennæ are *tactile* as are those in many other parts of the body. These are hollow outgrowths of the epidermis and its chitinous covering. Each contains the end of a nerve fiber prolonged outward from the dermis. There are two compound eyes at the front of the head, and since the latter is firmly fixed to the thorax, the eyes are raised on movable stalks.

Each *eye* is covered with the protecting, transparent cornea, the surface chitin; this is divided into very many four-sided facets. Beneath each facet is the eye proper, or ommatidium, optically separated from its neighbor by a black pigment. The outer portion of each ommatidium is the refractive vitreous body, which bends the light rays falling upon it downwards to the inner portion, the small retina. The retina is composed of very sensitive cells, the ends of the optic nerve fibers, and through these is connected with the brain. The pigment surrounding the ommatidium absorbs all light not reaching the nerve fibers, thus preventing a distortion of the image. Each separate division of the compound eye gives a complete image. The compound eye appears to be especially adapted for perceiving moving objects quickly and not for registering the form of the object.

Some delicate setæ upon the shorter, or anterior, pair of antennæ are supposed to function as organs of the chemical sense of smell-taste.

In the proximal segment of the shorter pair of antennæ occurs a sac-like inbending of the surface chitin. This sac, the *otocyst* or statocyst, is in free communication with the water outside through a small opening guarded by hairs. It is lined with sensory feathered setæ, similar in structure to the tactile setæ, and contains some minute sand grains. One function of this organ has been shown to be the maintenance of equilibrium, similar to that of the semicircular canals in man. Gravity acting upon these grains brings them into contact with different setæ as the body becomes tilted at different angles and through these setæ corresponding sensations are produced in the neighboring nerves which transfer them to the brain. Probably these setæ also take cognizance of the sound waves passing through the water and thus act likewise

as organs of hearing. When the animal molts, the chitinous lining of this sac is also shed so that new sand grains must be gathered after each molt.

Reproduction is sexual. The eggs are of considerable size with a large amount of yolk. They are fertilized immediately after extrusion and are fastened to the swimming legs of the female by a sticky secretion from glands on those appendages.

The one-celled egg after fertilization rapidly develops into the blastula stage and this into the gastrula. Thickenings then develop in definite parts, forming the rudiments of the three anterior appendages of the head; this is the nauplius stage. After this the embryo rapidly passes into the form in which it is hatched, that is, it becomes adult in form but not in size.

1. What is the present habitat of Cambarus?
2. Name the principal external divisions of the body.
3. What are the divisions of a typical appendage?
4. Is the skeleton internal, *i.e.*, covered upon the outside by a renewing fleshy layer, or external?
5. What is the composition of the skeleton? What difference in composition between the regions subject to bending and those not so subject?
6. Why is molting necessary to growth?
7. What parts of the body are thus renewed?
8. How often does molting occur? Describe the process.
9. Are the gills external to the body or internal? How are they protected?
10. Where are the muscles fastened? How does this differ from the muscles of the Vertebrata?
11. What are the principal muscles of the body? Give location and use.
12. How does the animal move?
13. Give three methods of progression used by the crayfish.
14. How do the muscles effect the complicated leg movement?
15. What does Cambarus eat? How is food procured?
16. Describe digestion; absorption.
17. Briefly trace the course of the blood through the body. What are its functions?

18. How does the crayfish breathe?

19. Give three means by which the waste of the body is eliminated.

20. Of what does the nervous system consist?

21. In effectiveness of response to environment, how does this system compare with that of the pelecypod? The coral?

22. What sense organs does Cambarus possess? Describe each.

23. Describe reproduction.

General Survey of Class Crustacea

Usually aquatic and carnivorous arthropods, with body divisible into head, thorax, and abdomen. The body is inclosed by a protective and supporting chitinous cuticle which becomes much thickened with lime carbonate where no movement is required. The food, consisting largely of decaying animal matter, passes through the mouth usually into a large stomach, thence into a straight intestine which opens to the exterior at the posterior end of the body. The anterior and posterior portions of the digestive canal are lined with chitin, which is continuous with that of the exoskeleton; only the middle portion is unlined and this alone develops outgrowths for secretion of digestive fluids and for absorption. A contractile heart forces the blood through the arteries to the surface of the body, whence it returns through the veins or open sinuses to the heart, passing on the way through the gills, where these are present. Respiration is by the general surface of the body or by gills (hollow offshoots of the thoracic walls or of the thoracic or abdominal limbs). The young usually passes through a series of larval stages — the nauplius, zoœa, and mysis stages. Through successive molts the young animal increases in length by the addition of new segments anterior to the telsonic region.

Abundant as fossils.

Derivation of name. — Latin *crusta*, a crust, referring to the hard, crust-like calcareo-chitinous skeleton completely inclosing the animal.

The class Crustacea is divided into the following subclasses:

Sometimes the Branchiopoda, Ostracoda, Copepoda, and Cirripedia are united into a single subclass, the Entomostraca.

SUBCLASS 1. TRILOBITA

Type of the subclass, *Triarthrus* (Fig. 155).

Triarthrus is much more closely allied to Apus (see p. 355) than to the crayfish, or any other living form, but lacks the peculiar carapace and probably the long anal processes of the former. These processes, however, are known to be present, extending backward from the ventral surface of the abdomen, in *Neolenus serratus* of the Burgess shale (mid-Cambrian) of British Columbia. The carapace is lacking in many species of the order Phyllopoda, to which Apus belongs; this is true of the fresh-water shrimp, Branchipus, and of the brine shrimp, Artemia, but in other respects these genera are more specialized and hence less like the trilobites than Apus.

Triarthrus, a trilobite crustacean, lived in the marine waters of eastern North America and northern Europe during the Ordovician period.

The body was entirely incased in a chitinous **skeleton,** hardened with more or less lime carbonate. Dorsally this skeleton was thickened, forming the *dorsal shield;* it is this which is usually preserved. It is divided into the head (cephalon), thorax, and pygidium; two furrows extend from the front of the head to the end of the pygidium, separating a higher, narrow median portion, the *axial lobe,* from a lower portion on each side, the two *pleural lobes.*

The portion of the axial lobe in the head is called the *glabella;*

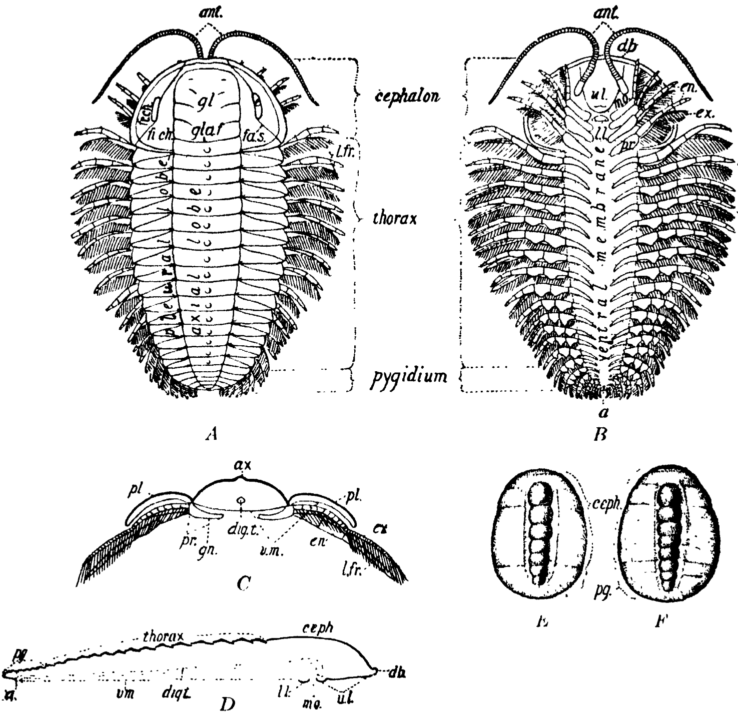


FIG. 155. — The trilobite, *Triarthrus eatoni* Hall (*T. becki*), from the Utica shales (mid-Ordovician of eastern North America). This species flourished in the muddy portions of the ocean which then covered this region. *A*, dorsal view. *B*, ventral view. *C*, a transverse vertical section at second thoracic segment (A–C $\times$ $1\frac{1}{3}$). *D*, a median longitudinal vertical section. *E* and *F* ($\times$ 45), two molts of the larval (protaspis) stage; the later molted one (*F*) has added to the pygidium an additional segment; in neither are any thoracic segments yet developed; the head has five segments with the eye-lines extending from the first segment. *a*, anus; *ant.*, antennules or feelers; *ax.*, axial lobe; *ceph.*, cephalon or head segment; *db.*, doublure; *dig.t.*, digestive tube; *e*, eye lobe protecting the compound eye; *en.*, endopodite; *ex.*, exopodite; *fa.s.*, facial suture; *fi.ch.*, fixed cheeks; *fr.ch.*, free cheeks; *gl.*, glabella; *gla.f.*, glabellar furrows; *gn.*, gnathobase (the free, inward projecting part of the protopodite); *l.fr.*, limb fringes, for swimming and respiration; *l.l.*, lower lip or metastome; *mo.*, mouth; *pg.*, pygidium, covering the abdomen; *pl.*, pleuræ; *pr.*, protopodite; *u.l.*, upper lip or hypostome; *v.m.*, ventral membrane. (All after Beecher, except *D*.)

it is large, well-defined, subquadrate, and marked usually by two pairs of discontinuous furrows (glabellar furrows). (Compare *gla.f.* in Figs. 155 and 156.) Extending from the posterior angles of the head shield obliquely toward the glabella and then anteriorly to the margin is the *facial suture* (compare *fa.s.* in Figs. 155 and 157), dividing the sides of the head shield into *free* and *fixed cheeks*, united by uncalcified chitinous joints.

The *thorax* is divided by transverse furrows into fourteen to sixteen segments, united by joints of chitin.

The *pygidium*, which covers the abdomen, consists of a single piece, though the superficial grooves divide it into axial and pleural lobes.

The head shield is anteriorly bent under and reflexed. To this reflected border, or *doublure*, was attached medially a separate plate, the upper lip, or *hypostome*. Posterior to this was a small convex plate, the lower lip, or *metastome*. The animal was further protected on the under side by a thin, uncalcified, chitinous membrane (Fig. 155, *B*) divided into an axial and two pleural portions corresponding to the axial and pleural lobes of the dorsal shield. This ventral membrane was attached to the upper and lower lips, to the reflected border of the head shield, to the pygidium, and to the ends of the pleuræ; it was further supported by transverse, calcified, chitinous processes to which the legs were attached.

Triarthrus is well called the "daddy longlegs" trilobite, for its **appendages** were unusually long for a trilobite, extending far beyond the margins of the dorsal shield. (In such forms as Trinucleus and Isotelus they did not extend to the margin of the dorsal shield.) These appendages were very uniform in character from the pair directly behind the antennules to the last pair upon the abdomen.

All except the most anterior pair of appendages, the antennules, are biramous, consisting of a basal portion: the protopodite bearing two branches: (1) the highly jointed endopodite adapted to crawling, and (2) the less jointed exopodite, fringed along its posterior border by lamellæ-like setæ and thus

adapted both to swimming and respiration. Anteriorly the endopodites are long, cylindrical, crawling legs; posteriorly they become more and more broadly flattened and leaf-like, bearing tufts of setæ; they are thus well adapted to swimming. Each protopodite has an inward projecting portion, the jaw-like base or gnathobase.

There were paired dorsal and ventral **muscles** beginning in the head and ending in the abdomen; the dorsal pair extended the animal, the ventral pair flexed it; but apparently it lacked the power of enrollment (p. 348). The ventral pair of muscles were separated by a chitinous ridge; from each of these a muscle band extended obliquely outward and backward to the next thoracic segment to be there attached, as is indicated by oblique chitinous ridges. The appendages were probably moved similarly to those of Apus and Cambarus.

Judging from the **food** of the living Crustacea, Triarthrus was carnivorous, eating both decaying and living animal matter. The food brought to the ventral median line of the body by the rhythmical movement of the appendages was seized by the gnathobases and by them carried forward to the mouth; the broader and stronger appendages of the head may, like the mandibles of Apus, have torn the food into smaller pieces. The mouth, opening between the upper and lower lips, led into a long intestinal tube which extended backward parallel to the dorsal test, opening through the anus at the postero-ventral end of the pygidium (Fig. 155, *D*). The digestion of food was probably similar to that of Apus, except that in the absence of a stomach the digestive fluid was probably poured into the anterior portion of the intestine.

Somewhat similar to the condition in Apus may likewise have been its *blood circulation*, *excretion*, its *nervous system*, and sense organs. The intestinal tube, as well as the double chain of nerve ganglia, heart, etc., were located beneath the axial lobe in the median line of the body.

Respiration took place mostly through the limb setæ or fringes, aided probably by an exchange of gases through the

chitinous covering of the ventral surface, which was apparently almost as thin as that covering the setæ.

The antennules were probably tactile organs. There is a pair of slightly raised, compound *eyes* situated at the inner edge of the free cheeks, while the neighboring border of each fixed cheek is raised into a small eyebrow-like mound, the eye lobe or *palpebral lobe* (see Fig. 157, *e.l.*).

For **reproduction** and development, see page 348.

1. Give the habitat of Triarthrus; its geologic range.
2. Sketch specimen; label cephalon, thorax, pygidium, glabella, axis, glabellar furrows, eye lobes, facial sutures, fixed cheeks, free cheeks, pleural lobes.
3. Is the skeleton external or internal?
4. What is its composition now? When living?
5. How did growth take place?
6. Does each entire fossil necessarily represent the death of an animal? Why?
7. After molting or after the death of the animal, separation at the uncalcified joints occurs rather quickly. Name the parts of the dorsal shield which would remain intact; your reasons.
8. Describe the ventral protection of the animal.
9. What ventral appendages were there?
10. Why are the ventral appendages so seldom found?
11. What were the principal muscles of the body? Where located? Their function?
12. What was the character of the food of Triarthrus? How procured?
13. Trace the food through the digestive canal and its digestion.
14. Give the probable character of the blood circulatory system; the nervous system.
15. What sense organs did Triarthrus possess?
16. How did it breathe?
17. By what means is the embryology of such a fossil form as Triarthrus known?
18. What is the protaspis? Its characters?
19. How did the trilobite increase in size from this early larval condition to the adult?
20. What reasons are there for believing that trilobites were bisexual?
21. What reasons for placing the trilobites in the class Crustacea?
22. Why are trilobites made a separate subclass, and that the most primitive?

General Survey of Subclass Trilobita

The trilobites are extinct marine crustaceans with the body divided into a variable number of segments, and entirely incased in a protective chitinous skeleton; this is thickened and hardened with lime carbonate where no movement is required, but thin and flexible in the intermediate spaces. These thin places act as joints and it is here that after the molting or death of the animal a rather easy separation of the skeletal elements takes place. The majority of trilobites are between one and three inches long.

Trilobites were undoubtedly marine, since they are always found associated with such forms as corals, crinoids, brachiopods, and cephalopods, the living representatives of which are wholly marine. They lived throughout the entire world during the Paleozoic, from the Cambrian to the Permian, inclusive.

The **skeleton** (Fig. 155) consists of a thick dorsal shield, a very thin ventral membrane, and the covering of the body appendages. The dorsal shield is divided into head (cephalon), thorax, and pygidium. The *head shield* comprises three pieces — a median one consisting of the glabella and fixed cheeks, and the two free cheeks, the three united by thin chitinous joints. The *free cheeks* may represent the pleuræ of one of the anterior head segments. The thoracic shield consists of many segments — transverse divisions, varying from two in Agnostus to twenty-nine in Harpes, all united by thin chitinous joints; each of these segments is made up of a central axial lobe and two pleural lobes firmly united into one piece so that movement took place only between the segments. The *pygidium* consists of a single piece, due to the welding of a number of similar segments.

On the ventral surface of the head are five pairs of appendages, all of which, except the anterior pair (antennules), are similar in appearance and function, differing thus from those of Apus (p. 356) and the crayfish (p. 332). There is a pair of appendages

also to each segment of the rest of the body, whether free or coalesced into the pygidium.

Muscles. — The bodies of many trilobites, as Calymene, possessed the power of *enrollment,* like the pill-bug among the isopod crustaceans at present. This was brought about by the contraction of the ventral muscles (p. 335). By this means the soft under surface was protected and the animal exposed to attack only along the hard dorsal shield.

Sight. — The organs of sight vary greatly among trilobites; when present they are situated on the free cheeks (except in Harpes, where they are on the fixed cheeks). A few genera, as Agnostus, and the larvæ of many forms appear to have been totally blind; others, as Conocoryphe, have small simple eyes, granule-like, at the end of a raised line (*eye-line,* Fig. 155, *F*) running from the anterior end of the glabella outward to the free cheeks. The majority of trilobites, however, had compound eyes of varying size; these either have (1) the separate facets covered by a continuous smooth or granular, horn-like, protective layer — the cornea, as in Calymene; or (2) each facet with a separate cornea, as in Phacops (Fig. 160, *C*).

Preservation. — Since the thin ventral membrane and delicate limbs were usually quickly destroyed after the molting or the death of an animal, they are very seldom preserved in the fossil state; and as sediment would cling readily to the angular ventral surface of the dorsal shield, the hardened sediment splits most easily along the comparatively smooth dorsal surface. Hence trilobites are almost always found as mere exteriors of the dorsal shield, and even this shield occurs comparatively seldom as a complete whole, for its parts are easily separable from one another.

Development. — Judging by existing Crustacea, reproduction among the trilobites was sexual. Frequently the same species shows a broad and a narrow form; the former may represent the female and the latter the male. The minute rounded bodies associated with many trilobite remains are regarded as possible trilobite eggs. The earliest stage in their develop-

ment definitely known is the larval form, named *protaspis.* This is believed to approach closely the proto-nauplius, the theoretical primitive larval form of all Crustacea, occurring as it does in the Lower Cambrian and possessed of such simple characters. The dorsal shield of this protaspis has been discovered in all the principal trilobite groups and its characters may be summed up as follows: minute, less than 1 mm. long, circular or ovate in outline, with distinct and more or less strongly annulated axial lobe. It consists of a large cephalon and a very small pygidium. The glabella has at the beginning, or after a few molts, five transverse grooves; eyes when present are anteromarginal or submarginal; free cheeks when visible are narrow and marginal. The pygidium has an axial lobe of one to several annulations; its pleural portion is smooth or grooved (Fig. 155, *E*, *F*).

The various *stages in the growth* of a trilobite have been studied by means of long series of specimens, separate molts of the same species but of differing sizes, just as the record of the growth of a crayfish may be read in the series of molts it discards. During growth, the body elongates through successive molts; the eyes when present move dorsally toward the glabella, and the free cheeks increase in size. Several molts take place before the introduction of the first thoracic segment, during which the glabella becomes more strongly annulated, the free cheeks appear on the dorsal surface, and the introduction of new appendages and segments to the pygidium produces in that additional grooves in the axial and pleural portions. The pygidium, in some genera, is completed before the introduction of the first thoracic segment. From the anterior edge of the pygidium are developed all thoracic segments and by the forward movement of this growing area the enlargement of the pygidium is effected. Apparently never more than one segment is added at each molt, but there may be more than one molt to each segment. In Triarthrus the full number of body segments was attained when the animal was about 7 mm. long; from then on it merely increased in size until adulthood, with a length of 25 to 40 mm..

was attained. The simplest protaspis is found in the Cambrian rocks; in later periods it acquires through acceleration in development adult characters such as dorsal movement of the eyes, free cheeks, etc.

Relationship. — That trilobites belong to the class Crustacea and are related to the subclass Branchiopoda (*e.g.*, Apus, p. 355), the most primitive of living Crustacea, is shown by the following characters common to both: (1) variable number of thoracic and abdominal segments among species of each genus; (2) slight distinction between thoracic and abdominal feet, each of which is more or less leaf-like and respiratory in character, is biramous and usually produced into a gnathobase; (3) five pairs of head appendages; (4) an upper lip (hypostome) and lower lip (metastome); (5) a pair of slender, jointed antennules.

Derivation of name. — Trilobita < Latin *tri*, three, + *lobus*, a lobe, referring to the division of the dorsal shield into three longitudinal portions, the axial lobe and two pleural lobes.

Paradoxides (Fig. 156). *Middle Cambrian.*

The portion of the animal found fossil is the strongly calcified dorsal shield, and very frequently also the upper lip (hypostome). The glabella of the dorsal shield enlarges anteriorly with its lobes well defined; the genal angles are usually produced into spines as are consequently likewise the tips of the pleuræ; the genal spines are borne by the free cheeks; the eye lobes are large and arched; the thorax has 17 to 20 segments; the pygidium is small and plate-like. The name was given by Brongniart in 1822 out of compliment to Linné's name for a trilobite — *Entomolithus paradoxus*, the paradoxical insect.

It is very abundant in eastern North America, Europe, and Australia.

1. Sketch specimen, labeling cephalon, glabella, eye lobes, genal spines, fixed and free cheeks, facial suture, thorax, axis, segments of thorax, pygidium.
2. Make an ideal sketch showing the relationship of the hypostome to the rest of the animal.
3. Why is this genus placed under the trilobites?

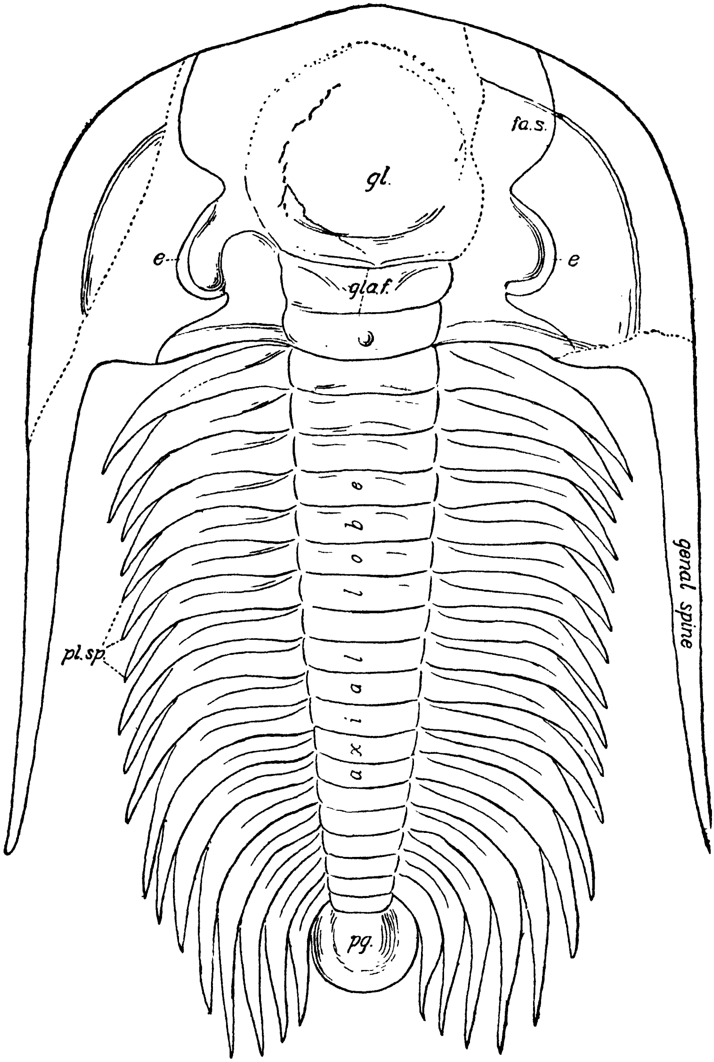


FIG. 156. — The trilobite, *Paradoxides harlani* Green (× $\frac{2}{3}$), abundant in the marine Braintree slates (Middle Cambrian) of eastern Massachusetts. *e*, eye lobe; *fa.s.*, facial suture; *gl.*, glabella; *gla.f.*, glabellar furrows; *pg.*, pygidium; *pl.sp.*, pleural spines. (Redrawn from Walcott.)

4. Was the skeleton external or internal? How much of the entire animal is preserved in the specimen sketched?

5. What was the composition of the skeleton in the living state? What is its composition now?

6. Does this specimen necessarily represent the death of an animal? Why?

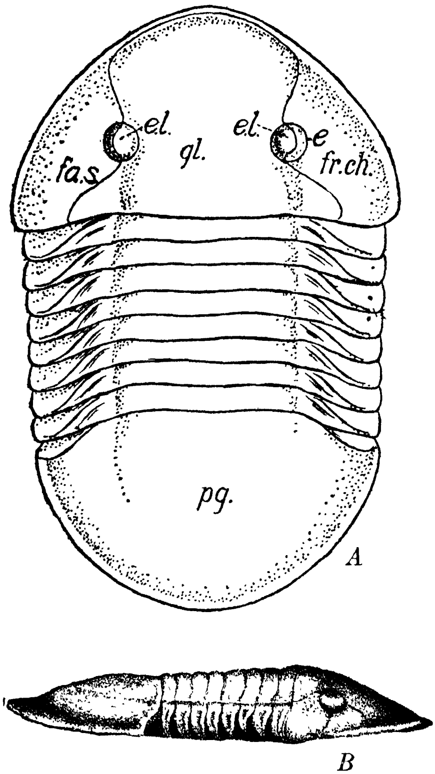


FIG. 157. — *Isotelus gigas* Dekay. Natural size. A Paleozoic mud-grubber. *A*, dorsal view of a broad form, possibly a female, of this species. *B*, a side view. *e*, eye; *e.l.*, eye lobe; *fa.s.*, facial suture; *gl.*, glabella; *pg.*, pygidium. (*A*, after Logan; *B*, after Hall.)

Isotelus (Fig. 157).

Ordovician.

Dorsal shield oval, its cephalon and pygidium large, subequal, with obsolete segmentation and wide flattened borders. The thorax has eight segments, with a broad and rather indistinct axial lobe. The smooth, shovel-like cephalon and pygidium and the lack of projecting spines seem to indicate an adaptation to plowing through the mud, like the modern horsehoe crab. The name was given by Dekay, 1824, in reference to the subequal cephalon and pygidium, from the Greek *isos*, equal, + *telos*, end.

Abundant in North America. *I. gigas*, a species abundant in the mid-Ordovician of North America, occurs very frequently with the dorsal shield entire.

1. Sketch specimen, noting glabella, eye lobes, thorax, pygidium.
2. How does this differ from Paradoxides in (*a*) glabella, (*b*) eye lobes, (*c*) axial lobe of thorax, (*d*) pygidium?
3. What is the significance of the name?

Cryptolithus (Trinucleus) (Fig. 158). *Ordovician.*

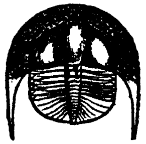


FIG. 158. — *Cryptolithus tesselatus* Green (*Trinucleus concentricus*). Natural size. The lace-collar trilobite, abundant in the Ordovician seas of North America and Europe. (After Logan.)

The dorsal shield, the part of the animal usually found fossil, possesses the following characters: the cephalon is very broad in comparison with its length, with long genal spines (borne by the free cheeks) and a regularly pitted border, whence its common name — lace-collar trilobite. The glabella is prominent, with a strongly convex area on each side, giving thus three prominent elevations to the cephalon. Eyes are usually absent; the thorax has six segments; the axial lobe is narrow.

It is abundant in North America and Europe.

1. Sketch specimen, labeling the portions preserved.
2. What is the significance of the common name?
3. What part of the living animal do fossils of trilobites represent?

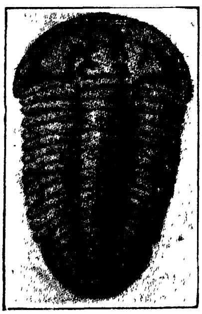


FIG. 159. — *Calymene niagarensis* Hall. A trilobite living in the seas of the Silurian period. Dorsal view. Natural size. (After Hall.)

Calymene (Fig. 159). *Ordovician to Devonian.*

Cephalon with a thickened margin, the facial suture cutting the lateral margin immediately anterior to the genal angle; the glabella is very convex, broadest behind, divided by three pairs of lateral grooves which define three rounded lateral folds decreasing in size anteriorly; the eyes are small. The thorax is divided into thirteen segments. Calymene is very frequently found enrolled like the living pill-bug,

showing that it possessed well-developed ventral muscles. By this means it protected the more vulnerable ventral surface of its body.

Calymene was probably a mud-grubber, like Isotelus. It is found in North America, Europe, and Asia. *C. niagarensis* is very abundant in the mid-Silurian (Niagaran) rocks of central and eastern North America.

1. Sketch specimen, labeling the various parts.
2. Why are these found so often in an enrolled state?
3. Of what advantage was this to the animal? Name a living animal which enrolls.
4. Are the eyes simple or compound? How do you account for the smooth surface?
5. During what eras did trilobites live?
6. Why are the legs of trilobites found so very infrequently?
7. Why is this genus placed under the phylum Arthropoda?

Phacops (Fig. 160). *Silurian to Upper Devonian.*

The dorsal shield has the following characters: (*a*) the cephalon is convex; the glabella is very wide in front, narrowing

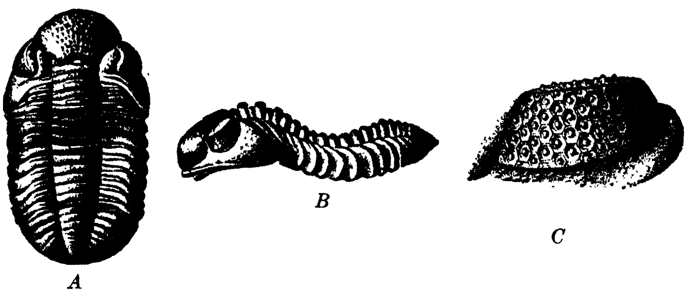


FIG. 160. — A trilobite. *Phacops rana* Green, from the Hamilton (Middle Devonian) formation of New York. *A*, dorsal view. Natural size. *B*, side view. *C*, an eye (× 3), showing the facets with their lenses preserved. (After Hall.)

behind, its anterior two pairs of lateral furrows indistinct; eyes very large, always with many distinct facets; the facial suture cuts the lateral margin of the cephalon anterior to the genal angle; (*b*) the thorax has eleven segments; (*c*) the pygidium is

semi-circular. The surface of the entire dorsal shield, especially the glabella, is often pustulose. The name, from the Greek *phakos*, lentil (lens), + *ops*, eye, refers to the many lens-like facets of the compound eyes.

This genus is abundant throughout the world. *P. rana* was abundant in the sea covering eastern North America during the middle of the Devonian period.

1. Sketch (*a*) specimen; (*b*) entire eye. Note glabella, facial sutures, eyes, eye facets, pygidium, pustulose surface.
2. What part of the entire animal does this fossil represent?
3. What is the significance of the name?
4. What differences between the eyes of Phacops and those of Calymene?
5. How does the glabella of Phacops differ from that of Paradoxides? from that of Calymene?
6. How does the relation between fixed cheek, facial suture, and genal angle differ in Phacops, Calymene, and Paradoxides?
7. From analogy with a living crayfish describe how Phacops molted.

SUBCLASS 2. BRANCHIOPODA (PHYLLOPODA)

Small, with elongate body segmented and covered anteriorly with a carapace. The great majority inhabit fresh water; Artemia lives in salt lakes and brine pools. Many produce two kinds of eggs, the parthenogenetic thin-shelled and the sexually produced thick-shelled ones, which latter alone can survive cold and desiccation. Known in the fossil state from the Cambrian to the present.

Derivation of names. — Greek *branchia*, gills, and *phyllon*, leaf, + *pous* (*pod*), foot. So named from the broad, flat, leaf-like feet which serve as gills.

Apus (Fig. 161). *Triassic to present.*

Apus is one of the most primitive of all living Crustacea; it is present, though not common, in the fresh waters of nearly every portion of the world and is found in the fossil state from the Triassic to the present.

In general appearance it differs from the crayfish in its broadly projecting oval carapace, in the pair of long processes at the end of the anal segment, in its small size (it is an inch or two long), in the variable number of body segments, and in the thinner and more flexible exoskeleton.

Apus is similar to the crayfish in the growth of the hard parts, in the presence of the upper and lower lips, and in the five pairs

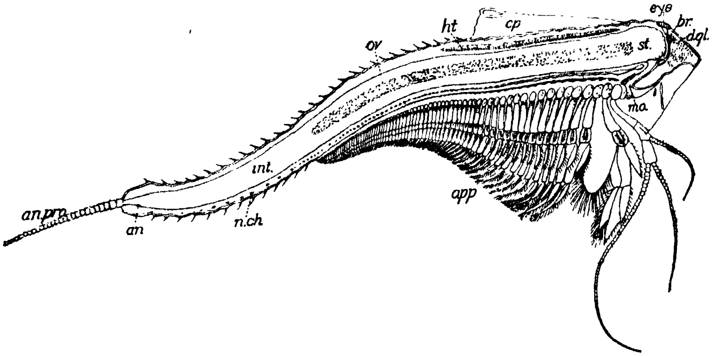


FIG. 161. — The primitive, fresh-water, recent crustacean, *Apus lucasanus* Packard, from Kansas. Section through the body, with intestine removed. Length of body, exclusive of anal processes, is twenty millimeters. *an.*, anus; *an.pro*, anal process; *app.*, appendages; *br.*, brain; *cp.*, carapace; *d.gl.*, digestive gland; *ht.*, heart; *int.*, position of intestine; *mo.*, mouth; *n.ch.*, ventral nerve chain; *ov.*, ovary; *st.*, position of stomach. (Redrawn from Packard.)

of head appendages, but is more primitive in having the posterior pair of cephalic appendages biramous, and in the practical absence of distinction between the thoracic and abdominal appendages. All of these except a few at the apex are leaf-like with a spinose projection (gnathobase) from the basal portion; these gnathobases, meeting the ones from the opposite side of the body, function as a conveyor of food to the mouth.

In the *muscular system*, its more primitive structure is shown by the arrangement of the muscles in a tube, as in the Annulata; they do not fill up most of the abdomen as they do in the crayfish.

The kind of *food,* its intake, the *digestive system,* absorption of food and excretion are similar to those in the crayfish. There is, however, but one division to the stomach, neither gastric mill nor sieve being developed. The digestive fluid is poured into the stomach.

In the absence of large claws most of the food is moved forward to the mouth by the long line of paired gnathobases, to which it is brought by the rhythmical movements of the appendages in swimming.

1. What is the habitat of Apus? Its geologic range?
2. How does it differ in general appearance from Cambarus?
3. In what respects is it more primitive than Cambarus, nearer the trilobites? Note (*a*) external appendages, (*b*) muscular system, (*c*) digestive canal.

Estheria (Figs. 162, 163). *Devonian to present.*

Carapace developed into a horny shell of two thin, rounded, inequilateral valves, united by a straight dorsal margin. The

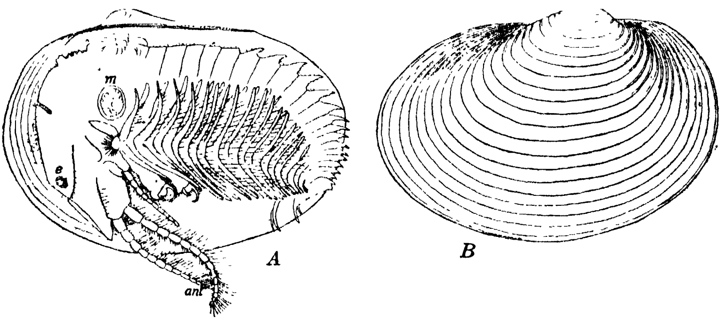


FIG. 162. — *Estheria belfragei* Packard, recent from Texas (× 5). *A,* the body of the animal shown after the removal of one valve. *ant.*, antenna; *e,* eye; *m,* adductor muscle. *B,* exterior of one valve. (Redrawn from Packard.)

surface of each valve is covered with concentric ridges, between which are interlacing striæ. The umbonal region sometimes bears a strong muscle node.

The modern species of Estheria live in fresh water, especially in ponds and rain pools, very rarely in brackish water. The concentric ridges, coarsest near the umbo, are due to the fact that "the integument of the outer surface of the shell is not cast off in ecdysis [molting], but remains in position, giving rise to a series of lines of growth marking the increased size of the shell at each molt." The spaces between the successive ridges are marked with irregular, interlacing striæ, differing thus from any pelecypod shell which the bivalved carapace otherwise closely resembles.

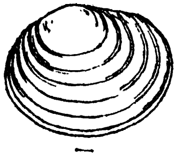


FIG. 163. — The minute phyllopod crustacean, *Estheria ovata* Lea, from the fresh-water Shinarump formation of southern Utah. (× 12; line below indicates true size.)

E. ovata is abundant in the Triassic of North America, such as the Newark beds of the Atlantic coast and the Shinarump of Arizona.

1. Sketch the outside of one valve.
2. How much of the body of the animal did the shell cover?
3. How can you tell from the fossil alone that this is a crustacean and not a pelecypod?
4. What is the origin of the concentric ridges?
5. Name three characters which distinguish crustaceans.



FIG. 164. — *Yohoia tenuis* Walcott (× 2) from the Middle Cambrian (Burgess shales) of British Columbia. In these fine-grained shales this primitive branchiopod crustacean is preserved in side view, showing segmentation of head and thorax, with antenna and some of the thoracic appendages. (After Walcott.)

Other examples of the Branchiopoda are Protocaris (Lower Cambrian, looking much like Apus), Yohoia (Fig. 164), Branchipus (living).

SUBCLASS 3. OSTRACODA

Minute, with body short, unsegmented or very indistinctly so, completely inclosed by the carapace which here becomes a

lateral, two-valved chitinous or strongly calcareous shell, usually 0.5–5 mm. long; this opens by means of an elastic, dorsal ligament and is closed by a large, subcentral adductor muscle. When closed the edges of the usually unequal valves as a rule fit closely, the edge of the one valve within a groove at the margin of the other. There is a median eye and at times also compound eyes. When the shell is strongly calcified so as to become opaque, more transparent spots in the antero-dorsal part of the shell mark the position of the eyes. The position of the adductor muscle is likewise usually noticeable upon the exterior of the shell as a group of spots. There are seven pairs of appendages which can be protruded when the valves open. The first and second pair of antennæ are large and are used for swimming or creeping. The outer surface of the valves is seldom smooth; usually it is covered with rigid hairs, or is pitted or sculptured. Sometimes the shell is notched anteriorly to allow the passage of the antennæ when the valves are closed. The posterior half of the shell is usually thicker than the anterior. The ostracod shell is distinguished from that of the pelecypod by its minute size, its usually unequal valves, its external sculpturing, the absence of concentric growth lines, and the presence of the eye spot on the exterior of the shell.

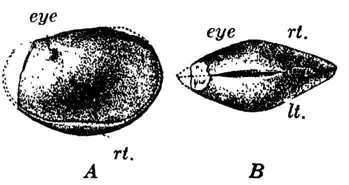


FIG. 165. — A fossil ostracod, *Leperditia alta* Conrad, from the uppermost Silurian of New York. The ends are imperfect. *A*, left valve (*lt.*) of the carapace, showing the incurving edges of the larger right valve (*rt.*), and the eye tubercle (*eye*), beneath which the eye was located. *B*, view of hinge margin. (Both × 2.)

Ostracods are abundant in marine, brackish, and fresh waters, usually creeping among the plants or burrowing in the mud. They are abundant in all ages from the Ordovician to the present; usually only the bivalve shell is preserved in the fossil. Cypris (living) is very abundant in stagnant pools.

Derivation of name. — Greek *ostrakon*, a shell, + *eidos* (*oid*), form; the carapace takes the form of a two-valved shell.

Leperditia (Fig. 165). *Ordovician to Devonian.*

Shell thick, smooth, biconvex, 2 mm. to 22 mm. long. Hinge line straight, usually angular at the extremities. Anteriorly, near the hinge, a small tubercle marks the position of the eye.

1. Sketch shell (*a*) view of one valve; (*b*) hinge view of combined valves. Label eye tubercle, ligament.
2. How much of the body of the animal did the shell cover?
3. Why is this bivalve shell placed under the Crustacea and not under the Pelecypoda? How can this be told from the fossil alone?
4. Compare the shell of Leperditia with that of Estheria (a branchiopod). How do they differ?
5. What opens the valves? What closes them?

SUBCLASS 4. COPEPODA

Body elongate, segmented, covered with a carapace; thorax usually with four or five pairs of biramous feet; abdomen free from appendages. Copepods are mostly marine, though many inhabit fresh water. Very many are parasitic, especially on fish; few fish are entirely free from them. Name from Greek *cope*, oar, + *pous* (*pod*), foot. So named because their feet are used mostly for swimming. Unknown in the fossil state.

Two kinds of copepods occur: (*a*) parasitic, *e.g.*, carp lice (Argulus); (*b*) free-swimming, *e.g.*, water fleas (Cyclops). Under favorable conditions one cyclops might have five billion descendants in one year. In this form anal respiration is especially noticeable. This method of breathing, common among the lower Crustacea, consists of rhythmical contractions of the intestine, which admit and expel the water.

SUBCLASS 5. CIRRIPEDIA (BARNACLES)

Body imperfectly segmented; posterior part of trunk vestigial. The carapace of other Crustacea here forms a fleshy mantle, usually strengthened by calcareous plates.

These degenerate animals are marine, and fixed during adult

life, or they are parasitic. The fixed forms have the body and limbs completely inclosed in a mantle strengthened by calcareous plates. They are attached by the anterior part of the head either by a flattened disk (as in the sessile or acorn barnacle, Balanus), or by an elongate, muscular stalk (as in the goose or ship barnacle, Lepas).

Barnacles are a very interesting example of *degeneracy*, their life history passing from a free-moving youth to an attached maturity, accompanied by a degeneration of the body until the whole posterior portion becomes vestigial. The young larva is free-swimming, hatched as a free nauplius; after several molts this passes into the Cypris stage, with a bivalve shell like an ostracod but with limbs and internal anatomy unlike this subclass. Later it attaches itself to some object by its antennules aided by a secretion poured out from a gland at their base; soon the parts of the new, changed shell appear beneath the old one, which is molted, and the adult form is thus attained.

The Cirripedia are known from the Ordovician to the present, but have been abundant only since the upper Tertiary.

Derivation of name. — Latin *cirrus*, a fringe, + *pes*, foot; referring to the fringe-like feet which the animal can protrude from its shell and by means of which it respires and gathers food.

Examples are Balanus (Eocene to present; attached to rocks between tide levels), Lepas (Pliocene to present; growing on the bottom of ships, etc.), Tubicinella (living deeply embedded in the skin of whales), Anelasma (living embedded in the skin of sharks and partially parasitic by means of roots), Sacculina (living entirely parasitic on crabs, its roots penetrating all parts of the body except heart and gills). Probably the best known of all of these is *Balanus balanoides* which grows in such immense numbers over the whole northern Atlantic coast that it frequently covers the rocks.

1. Distinguish between the calcareous skeleton of the acorn barnacle and the skeleton of the goose barnacle. Give their geologic range.
2. Briefly trace the development of a barnacle.

3. Compared with its own larval state, is the adult advanced or degenerate? Why?
4. What is the habitat of living barnacles?

SUBCLASS 6. MALACOSTRACA

These scavengers of the sea-bottom have the body usually divided into a thorax of eight and an abdomen of seven segments. A gastric mill for grinding the food is present. Excretory organs are glands in the antennæ. The nauplius stage is usually passed through in the egg. Known in the fossil state from the Cambrian to the present.

Derivation of name. — Greek *malakos*, soft, + *ostrakon*, shell; so named because the carapace or shell is softer than the shell of the mollusk.

This is subdivided into the following orders:

The old order Schizopoda comprised the three very distinct orders — Anaspidacea, Mysidacea, and Euphausiacea.

(*a*) Nebaliacea (called also Leptostraca and Phyllocarida) — the most primitive branch of the Malacostraca. (Cambrian to present), a connecting link between the Branchiopoda and Copepoda on the one hand and orders *d–f* on the other. Examples, Ceratiocaris (Ordovician and Silurian). Nebalia (living). (*b*) Anaspidacea (Pennsylvanian to present). A well-known example is Paleocaris from the Pennsylvanian coal measures of North America and England. (*c*) Mysidacea (Mississippian to present). (*d*) Cumacea (not known fossil). (*e*) Isopoda (Devonian? to present), body flattened from above downwards. A common living example is the pill-bug (Armadillium); this is found in damp places under boards and stones and when disturbed rolls itself up into a ball. (*f*) Amphipoda (Silurian? to present), body flattened from side to side, *e.g.*, beach-fleas. (*g*) Euphausiacea (not known fossil).

(*h*) **Decapoda.** *Triassic to present.*

The posterior five pairs of thoracic legs are long and are used in walking, whence the name from Greek *deka*, ten, + *pous* (*pod*),

foot. The abdomen may be long and straight as in the lobster and crayfish or permanently flexed beneath the long cephalothorax, as in the crab group (examples 4–6). The latter group include the most advanced of all Crustacea. No undoubted decapods have been found in the Paleozoic, but their ancestors are to be sought for in the generalized schizopods (orders *b*, *c*, and *g*) of that era, and were probably not differentiated from the latter until the Triassic.

Examples: (1) Cambarus (Fig. 152). Crayfish of the family Astacidæ, to which Cambarus belongs, have been found from the Cretaceous to the present day. The distinction of Cambarus from Astacus, the other genus of this family, lies in the character of the gills, features not preserved in the fossil forms known. The crayfish is descended from marine lobster-like ancestors. (2) Homarus (Cretaceous to present). *H. americanus* (Fig. 154), the single Atlantic coast species of the American lobster, ranges from North Carolina to Labrador and from near shore to a depth of 100 fathoms. It is omnivorous and is attracted to its food mostly by the sense of smell. A female seventeen inches long will lay at one time about 60,000 eggs. The young pass through a stage in which they resemble the Mysidacea. The lobster molts about eight times the first year, five the second, and three the third. (3) Eryon (Jurassic to Cretaceous). (4) The Japanese spider crab (*Macrocheira kämpferi*) is the largest living crustacean, with at times a spread of legs of 18 to 20 feet. (5) The blue or edible crab (*Callinectes sapidus* or *hastatus*) ranges from Florida to Cape Cod; it prefers muddy shores and like the lobster lives largely upon decomposing animal matter. It molts at least once during the summer, at which time it is sold in the markets as a "soft-shelled crab." When raised for commercial purposes it is usually kept floating in a box until molting occurs. (6) Lobocarcinus (Eocene). This has a broad carapace, arcuate and much lobed in front.

(*i*) **Stomatopoda.**

The thoracic legs bend forward towards the mouth, whence the name from Greek *stoma*, mouth, + *pous* (*pod*), foot. Known

in the fossil state from the Pennsylvanian to the present. The mantis shrimp, Squilla (Jurassic to present), ranges from Cape Cod to Florida.

1. What is the geologic range of the members of this subclass?
2. Give a common example of the order Isopoda. Its habitat.
3. In what orders and era are the ancestors of the decapods to be sought?
4. Name four living and one fossil example of the decapod crustaceans.
5. How many eggs does a lobster lay at one time?
6. What is a "soft-shelled" crab?
7. What part of a malocostracan is most apt to be preserved in the fossil state? Why?

CLASS B. ONYCHOPHORA

This class includes the single genus Peripatus containing about 50 species. It is confined to isolated regions in the southern Hemisphere and the West Indies. It looks much like a caterpillar and is a typical arthropod except in its excretory and nervous systems, in which it approaches the Annelida and flatworms. Of this very primitive class no fossil representatives are yet definitely known, though a form from the Middle Cambrian Burgess shale of British Columbia resembles Peripatus rather closely.

Derivation of name. — Greek *onyx*, a claw, + *pherein*, to bear, in reference to the pair of horny claws terminating each foot.

CLASS C. MYRIAPODA

Body worm-like, of many similar segments, each bearing one (in centipedes) or two (in millipedes) pairs of legs (whence the name from Greek *myrioi*, 10,000, + *pous* (*pod*), foot). Skin stiffened with chitin, legs jointed. Head distinct, bearing a pair of eyes. Respiration by tracheæ like those of insects. Found from the Devonian to the present day.

The Myriapoda include (*a*) the centipedes (Chilopoda) (*e.g.*, Lithobius, of world-wide distribution, living on earthworms,

insects, etc.); (*b*) the millipedes (Diplopoda) (*e.g.*, Julus, the thousand-legged or galley-worm, carnivorous like Lithobius; when at rest it coils its body).

CLASS D. ARACHNIDA

Body usually divided into cephalothorax and abdomen; six pairs of legs (except in order Limulava) about the mouth, four of which at least are used in walking, the first usually bearing claws. No antennæ present (except in Limulava); eyes sessile, usually simple; in orders 1 and 2 both simple and compound eyes occur, in order 3 compound eyes only. Respiration by tracheæ (see page 372), book-lungs, or book-gills.

In the *book-lung* each opening leads into an internal chamber, the lining membrane of which has been folded into very many delicate laminæ, lying parallel with one another like the leaves of a book. The air circulates between the leaves, thus giving oxygen to the blood which circulates through each leaf. *Book-gills* are similar to book-lungs, but are external, attached to the abdominal appendages.

Relationship. — The class Arachnida typically includes a water-breathing division — the orders Xiphosura, Eurypterida, and Limulava (often placed together in the subclass Merostomata) — and an air-breathing division — the remaining orders. That these two divisions are intimately related is best shown in comparing Limulus, a water-breather, with Scorpio, an air-breather. These agree in the possession of the following characters: six pairs of limbs about the mouth, the anterior pair chelate; first pair of abdominal segments forming an operculum, with the genital aperture beneath it; the following five segments (except the first in Scorpio) respiratory in function; a ventral shield; paired median and lateral eyes; a vibratile spermatozoön (no crustacean except the Cirripedia have such). They agree also in the absence of antennæ. The book-gills of the former are replaced by the book-lungs of the latter (probably developed

through invagination, these in turn giving rise to the tracheæ of the other Arachnida). Both have a post-anal spine and in both the anus opens on the segment anterior to this, but this is in Scorpio the twelfth abdominal segment and in Limulus the seventh, the other five being absent. The embryo of the latter, however, when hatched, *i.e.*, during its three-lobed stage, shows the eighth pair well developed and an indication of the ninth. In Neolimulus of the Silurian period there are at least nine abdominal segments, while the Eurypterida (Cambrian to Permian) possess twelve abdominal segments besides the post-anal spine, in this being the exact parallel of Scorpio.

The eurypterids, Limulus and the scorpions, are thus intimately related. The limulids and eurypterids had already diverged in pre-Cambrian times. The scorpions likewise developed very early. The Silurian scorpions — Palæophonus, etc. — represent apparently the persistence of a group intermediate between the typical modern scorpion and Limulus or Eurypterus; this is seen particularly in the appendages. The apparent absence of spiracles in these early scorpions indicates that they had not yet taken to a life out of water. This derivation from a life in the water is corroborated in the ontogeny of the living Scorpio, where the book-lungs of the adult are derived from gills borne upon abdominal appendages in the young. Of these three orders the Eurypterida is the most primitive; but the evidence now at hand apparently indicates that the three have descended from a common ancestor and not from one another.

Derivation of name. — Greek *arachne*, a spider, referring to the typical example of this class.

The Arachnida are subdivided into the two subclasses Merostomata and Embolobranchiata.

SUBCLASS A. MEROSTOMATA

The water-breathing portion of the arachnids. This includes the orders Xiphosura, Eurypterida, and Limulava.

Order 1. Xiphosura (including Synxiphosura)

Body trilobed by longitudinal furrows. Cephalothorax covered by a large, semicircular carapace. Abdomen of seven to ten segments including the long, movable spine-like terminal segment, the telson. In at least some genera there are simple eyes present in addition to the compound eyes. Respiration by lamelliform gills (book-gills) attached to the abdominal appendages. Marine and fresh-water dwellers. Known from the Cambrian to the present.

This order, in some of its genera, resembles the trilobites but differs in the presence (at least in most of the genera) of both simple and compound eyes, in the absence of free cheeks and of an annulated pygidium, and especially in the character of its appendages, such as the presence of book-gills instead of limb fringes for respiration, and six pairs of legs about the mouth instead of a pair to each segment.

Derivation of name. — Greek *xiphos*, sword, + *oura*, tail; referring to the sword-shaped tail or telson.

The best known example is the horseshoe crab, *Limulus polyphemus* (Fig. 153). In this the six pairs of appendages are all chelate except the sixth, which is surrounded with whorls of plates which aid in pushing the animal over or through the mud. Of the seven abdominal segments, the six anterior ones consist of operculum and five pairs of book-gills; there are over one hundred pairs of gill leaves in all. This species lives in shallow water, grubbing in the mud for its food. It ranges from Yucatan to Maine. The eggs hatch in July and August. The young are trilobed like the trilobites; they swim much upon their backs. This is the last surviving genus of an order whose members were abundant both in number of genera and species throughout the world from early Cambrian times. (See relationship of the Arachnida, p. 365.) The only other living species (*L. molluccanus*) occurs off the east coast of Asia and in the Malay Archipelago. Limulus occurs from the Triassic to the present. The many other representatives of this order exist only as fossils,

as Belinurus (Devonian to Pennsylvanian), Neolimulus (Silurian), and Aglaspis (Cambrian).

1. Sketch the horseshoe crab, side view, showing one-half of the dorsal carapace. Label carapace, compound eye, telson, book-gills, operculum, legs.
2. Where does Limulus live? How?
3. Why is it placed under the Arachnida, and not under the Crustacea?
4. What is its geologic range?
5. Why do we expect an order with but a single living genus to have had a long ancestral history, with many fossil representatives? Mention examples of this among plants.

Order 2. Eurypterida

Body elongate with comparatively small cephalothorax and an abdomen of thirteen segments, including the post-anal telson. There are two large, lateral, faceted eyes, and a pair of median, simple ones. Six pairs of legs surround the mouth, the first pair probably always chelate, and the last pair, the broad, powerful paddle, used in swimming and in burying itself in the mud. The anterior six abdominal segments consist of the anterior genital operculum and the posterior five pairs of broad, leaf-like appendages, probably respiratory; these six are apparently comparable to the operculum and book-gills of Limulus (see relationship of the Arachnida, p. 365). The mode of life was varied; it included swimming, crawling, and burrowing. Eurypterids flourished from the Cambrian to the Permian, and were probably inhabitants of rivers and lagoons.

Though the order is entirely extinct, yet the *growth stages* of many of the Eurypterida are well known. In the Shawangunk grit (Middle Silurian) of southeastern New York excellent series have been obtained, some of the stages measuring less than two millimeters in length. The larval stages have a comparatively larger carapace, with compound eyes larger and nearer the margin, swimming legs usually larger, and a smaller number of segments to the body. The later larval stages

of the mid-Paleozoic species show some characters that are present in the adult Cambrian and Ordovician forms.

Some forms, as Pterygotus, attained at times a length of nine feet. Stylonurus is another large form from the Silurian and Devonian, distinguished by the possession of two pairs of enormously elongated appendages.

Derivation of name. — Greek *eurys*, broad, + *pteron*, wing, referring to the broad, wing-like pair of legs.

Eurypterus (Fig. 166). *Ordovician to Permian.*

Abdomen, including the telson, about five times as long as the subquadrate cephalothorax, which is bordered by a narrow furrow. Compound eyes reniform; the simple ones between these are close to the median line. First pair of head appendages very small; second to fourth pairs covered with spines; the sixth or last pair very large.

1. Sketch Eurypterus, dorsal view, noting both simple and compound eyes, cephalothorax, telson, appendages if present.
2. Describe its habitat and probable mode of life, giving reasons for your views.
3. How can the ontogeny of an extinct animal like Eurypterus be known?
4. In what respects do the larval stages of this genus differ from the adult?
5. What is the significance of the name Eurypterus?

Order 3. Limulava

An imperfectly known marine order from the Middle Cambrian. Attached to the short cephalothorax are a pair of long, simple, jointed antennæ similar to those of trilobites, and four pairs of other appendages, some of which are likewise trilobite-like in being biramous. The broad, tapering abdomen of twelve segments ends in a compound fin-like telson similar to that of the decapod crustaceans. Compound eyes only are present. This order may represent species transitional between the primitive arachnidan order Eurypterida and the primitive crustacean order Trilobita. The best-known genus is Sidneyia from the Stephen formation of British Columbia.

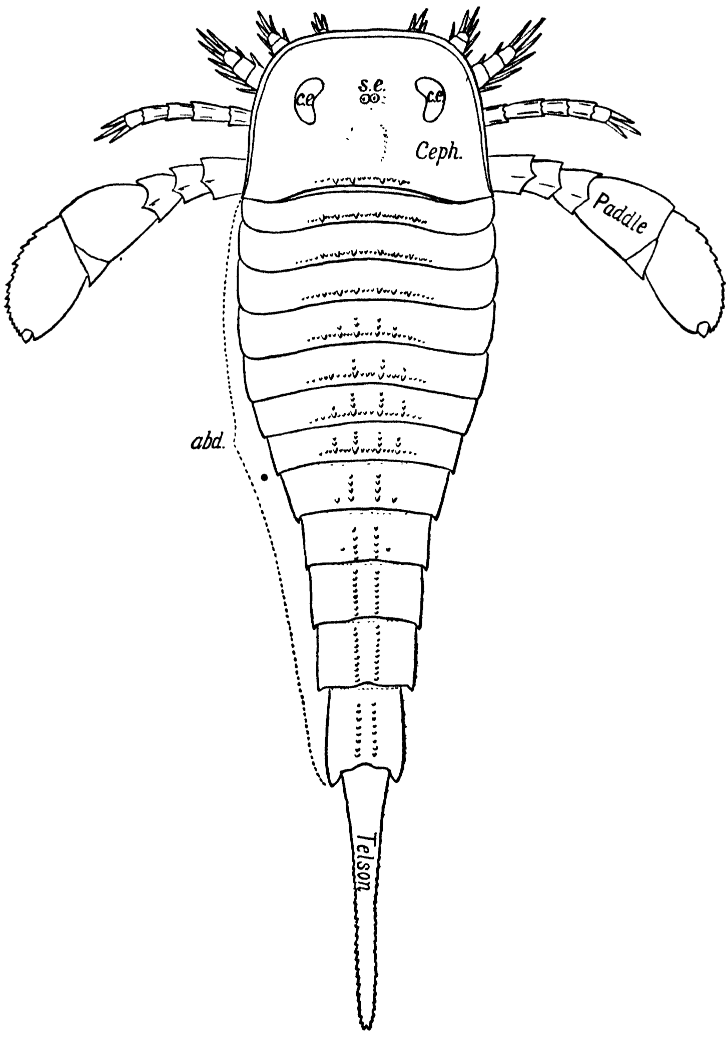


FIG. 166. — A water breathing representative of the class Arachnida, *Eurypterus remipes* Dekay, from the Bertie formation (mid-Silurian) of New York. Dorsal view (× ½), showing the compound eyes (*c.e.*) and the simple ones (*s.e.*) upon the cephalothorax (*ceph.*), five of the six pairs of legs, and the abdomen (*abd.*). (Redrawn from Clarke and Ruedemann.)

SUBCLASS B. EMBOLOBRANCHIATA

The air-breathing portion of the arachnids. Respiration by book-lungs or tracheæ. This includes a variable number of orders, only four of which are listed here.

1. Scorpionida (Silurian to present). The telson is modified to form a poison gland and sting. The scorpions have decreased since their maximum development in the Upper Paleozoic. *2.* Araneida (Pennsylvanian to present). Cephalothorax and abdomen are distinct but neither is segmented. At the posterior end of the abdomen are tubes (spinnerets), the tips of each perforated by very many openings from which comes a fluid which hardens upon contact with the air; the union of these hundreds of microscopic threads forms the ordinary thread just visible to the naked eye. This order includes the true spiders. *3.* Phalangida (Pennsylvanian to present). A well-known example is daddy longlegs (Phalangium); this lives upon small insects. *4.* Acarina (Oligocene to present). Degenerate arachnids. These include the mites and ticks.

1. Distinguish the Arachnida from the Insecta.
2. What difference between the water-breathing and air-breathing divisions of the Arachnida? What subclass names have been given to these two divisions?
3. Distinguish between book-gills, book-lungs, and tracheæ. Name animals of which these are characteristic.
4. Compare the branchiate Limulus with the tracheate Scorpio. In what respects do they (*a*) agree, (*b*) differ?
5. In what respects do fossil scorpions from the Silurian unite still more closely these branchiate and tracheate portions? How is this corroborated by the ontogeny of the living Scorpio?
6. What fossil forms agree with Scorpio more closely in abdominal segments?
7. Are the trilobites related to the limulids, eurypterids, or scorpions? Reasons.
8. What orders does the subclass merostomata include?
9. How early in geologic time are the Scorpionida known? the Araneida?
10. How is a spider's thread formed?

CLASS E. INSECTA

These six-footed arthropods have a body consisting of head, thorax, and abdomen, with the skin hardened by chitin. To this hardened skin, as in all other Arthropoda, the muscles are attached. The head bears normally a pair of feelers or antennæ, a pair of mandibles and two pairs of maxillæ, and usually a pair of compound, sessile eyes (the house fly has 4000 facets (*i.e.*, individual eyes) to each eye; the dragon fly 28,000). The eye in the insects, as in all invertebrates and even in the fish, salamanders, and frogs, functions principally to distinguish movement, that is, to tell the difference between living and lifeless objects. The dragon fly, for example, perceives only moving prey. The thorax has a pair of unbranched legs to each of its three segments and usually two pairs of wings. The abdomen of seven to eleven segments has no appendages. Since the wings are merely expansions of the chitinous skin stretched over chitinous tubes, the veining, these are often preserved in the fossil state notwithstanding their extreme delicacy. These tubes consist of a tube within a tube, the inner carrying air, the outer blood.

Respiration is by *tracheæ* — a system of air-tubes held open by elastic, spiral threads, penetrating all parts of the body and terminating upon the surface of the body in several button-hole-like openings, the stigmata; by the expansion of the abdomen air is drawn in through the stigmata and forced throughout the body; the contraction of the abdomen forces the air out again. Thus air is taken directly to all parts of the body instead of indirectly as in the vertebrates, where the blood acts as carrier of oxygen from the lungs. There is accordingly no need for either arteries or veins, though there is an elongate tubular heart situated in the dorsal part of the abdomen, which aids the movements of the body in transferring the blood and with it the digested food particles to all parts of the body.

The **sexes** are separate. Development is usually accompanied by *metamorphosis*. For example, the house fly lays 100 to 200

eggs in decaying animal matter, such as a manure pile; these in warm weather hatch into larvæ ("maggots") which, living upon this putrid matter, become fully grown in about one week, when each surrounds itself with a brown case (pupa case), from which it bursts a week later as a full-grown fly.

The majority of insects preserved as fossils were probably drowned and then covered with silt or other protective material, before they had time to decay. There are thus many of their remains found in coal, lignite, peat, amber, and ash deposits in ancient lakes. The following are some of the localities where the delicate bodies of insects, arachnids, and myriopods occur well preserved: Pennsylvanian of Commentry, central France; Saarbrücken, southwestern Rhenish Prussia; Mazon Creek, Illinois; Rhode Island Coal Measures; Permian of Kansas and New South Wales; Triassic of Queensland; Jurassic (lithographic limestone) of Solenhofen, Bavaria; Oligocene of East Prussia and Baltic amber; Miocene of Oeningen, Baden, on Lake Constance, and that of Florissant, Colorado.

Derivation of name. — Latin *in*, into, + *secare*, to cut. Originally named from such forms as bees and wasps, which are almost completely cut into two or three parts.

Summary of the Orders of Insecta

Insects are classified according to the method of their development into: (*a*) the ametabolous (*a*, not, and *metabola*, metamorphosis) insects. They are essentially like the adult except in size, when they are hatched from the egg. (*b*) The heterometabolous insects, in which the young resemble the adult except for the difference in proportion of various parts of the body, the absence of wings, etc. The wings develop outside the body. Thus the metamorphosis is direct (incomplete). Insects in both of these divisions remain more or less active throughout their development. (*c*) The holometabolous insects pass through both a larval and a pupal stage in their development (example, the fly, p. 372). In these insects the larval form is entirely

different from the adult and these stages are separated by a quiescent condition (the pupa). The wings develop within the body until the pupal stage; thus the metamorphosis is complete.

No undisputed insect has been found earlier than the Pennsylvanian. The earliest known insects are all heterometabolous and comprise orders now totally extinct. Some of these, like the Paleodictyoptera (Fig. 167), exhibit the combined characters of several of the most generalized living orders. In the Pennsylvanian appear also huge ancestral dragon flies (the first true dragon flies are found in the Lower Permian), Hemiptera, and probably ancestral Hymenoptera and Orthoptera. Of the last order, cockroaches formed an extremely abundant group in the coal-forming swamps, and persisted through the Permian, after which they declined to the present. Even to-day 1200 species are known, mostly tropical. The cockroach is one of the most interesting of our insects, being very primitive and with a family pedigree which extends back into the Pennsylvanian.

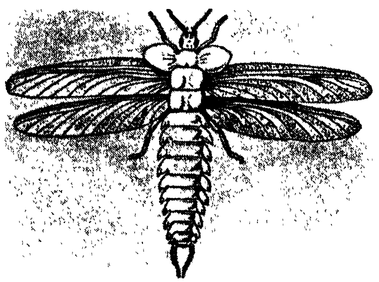


FIG. 167.—Stenodictya. A primitive insect from the Pennsylvanian period, belonging to the Paleodictyoptera order. The presence of lateral winglike outgrowths on each segment below the true wings suggests that the still more primitive ancestors of these insects may have possessed functional appendages on all segments, of which only the two pairs on the thorax and the small pair anterior to these on the prothorax survived as wings. (After Handlirsch from Tothill.)

In the Upper Permian appeared the first Coleoptera, Neuroptera, and possibly ancestors (the Paramecoptera) of the Lepidoptera, Trichoptera, and Diptera. True Diptera and Trichoptera appeared in the Jurassic, true Hymenoptera in the Cretaceous, and Lepidoptera in the Oligocene. Beginning with the Miocene, some genera now existing appeared.

Over 450,000 species of living insects have been described and

thousands of new ones are added yearly. Their classification is based primarily upon characters appearing in metamorphosis, wings, and mouth parts. Living insects are usually divided into 19 orders.

(*a*) **The ametabolous insects.** — *Order 1.* Aptera (wingless). This includes the Thysanura, the most primitive insects, but not found fossil until the Tertiary.

(*b*) **The heterometabolous insects.** — *Order 2.* Ephemerida, may-flies. *Order 3.* Odonata, dragon flies, damsel flies. *Order 4.* Plecoptera, stone flies (the young live beneath stones in brooks). *Order 5.* Isoptera, termites. *Order 6.* Corrodentia, book lice, bark lice. *Order 7.* Mallophaga, biting bird lice (chickens take dust baths to rid themselves of one species of these lice). *Order 8.* Thysanoptera, thrips. *Order 9.* Euplexoptera, earwigs. *Order 10.* Orthoptera, cockroaches, walking sticks, grasshoppers, locusts, crickets. *Order 11.* Hemiptera, lice (parasitic on man and other mammals), plant lice, scale insects, cicadas, spittle insects, bed bugs (these have acquired a taste for human blood), chinch bugs, squash bugs, stink bugs, and various aquatic forms, such as water boatmen, giant water bugs, and pond skaters. The last group (the Hydrometridæ) dwell upon the surface of water, a covering of dense velvety pile rendering their bodies incapable of getting wet and serving to retain a coating of air when submerged (which is then used in respiration).

(*c*) **The holometabolous insects.** — *Order 12.* Neuroptera, ant-lions, dobson flies. The larval stage of *Corydalis cornuta* in the latter group is known as hellgramite and is extensively used as bait by anglers; it is usually found beneath stones in streams and lives about three years before attaining the pupa stage. *Order 13.* Mecoptera, scorpion flies. *Order 14.* Trichoptera, caddis flies. The aquatic larva builds a case of leaves, twigs, or sand grains as a means of protection. *Order 15.* Lepidoptera, butterflies (Fig. 168) and skippers (both possess a knob-like swelling near the end of the antenna), moths (without the knob on the antenna). The larvæ of the Geometridæ family of moths are

called measuring worms. *Order 16*. Diptera, flies. There are about 7000 species in North America, including house flies, horse flies, blow flies, fruit flies, mosquitoes, crane flies, midges. *Order 17*. Siphonaptera, fleas. The human flea, *Pulex irritans*, is found all over the world. The jigger, or chigoe flea, burrows into the skin of man. *Order 18*. Coleoptera, beetles (Fig. 169). Examples, the potato-beetle (potato-bug), lady-birds, and scavenger beetles (family Scarabæidæ); this

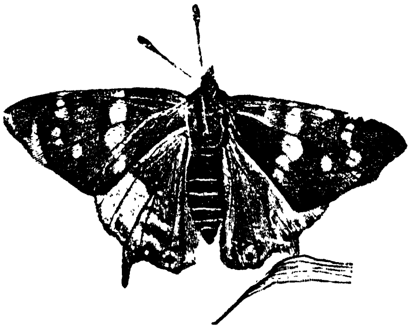


FIG. 168. — The butterfly, *Prodrya persephone* Scudder, from the Miocen shales of Florissant, Colorado. In thi specimen are marvelously preserved no only the knobbed antennæ and entir form as though mounted in a cabinet but the very scales upon the wings (From Scudder.)

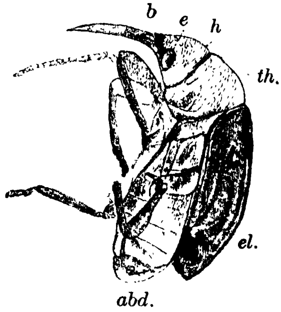


FIG. 169. — A beaked insect, *Teretrum primulum* Scudder, of the order Coleoptera, from the Miocene of Florissant, Colorado. Length 3 mm. *b*, beaks, not well preserved (the point of the beak was most probably rounded); *e*, eye; *el.*, *elytra* (the thick anterior pair of wings serving only as a protection of the posterior pair); *h*, head; *th.*, thorax; *abd.*, abdomen. (From Scudder.)

includes the sacred Scarabæus of Egypt and our common tumblebug. *Order 19*. Hymenoptera, about 7500 species known in the United States, including gall flies, bees (Apidæ), wasps (solitary and social), ants. Many of the ants have a complex social life.

1. Why are insects classed within the phylum Arthropoda?
2. What characterizes an insect?
3. In what respects are the eyes of most insects like those of most trilobites?

4. Account for the fossil preservation of the delicate veining in the wings of insects.
5. How does an insect breathe? How does this differ from the respiration of a vertebrate?
6. What is meant by metamorphosis?
7. Outline the development of the house fly.
8. Name some localities famous for the preservation of such delicate bodies as those of the Insecta and Arachnida.
9. Distinguish the three main divisions of insects. Give an example of each.
10. Why are dragon flies and cockroaches of interest to a paleontologist?

Evolution of the Arthropoda

Arising from some group of water-dwelling, primitive annelid worms during the Proterozoic, the arthropods retain the annelid structure of the nervous system and the mode of growth of the body segments, with the consequent segmented elongated body. From this primitive arthropod group arose independently, according to present belief, the trilobites, the branchiopods, and the arachnids.

The trilobites are the most primitive and most generalized representatives of the arthropods. They radiated rapidly into bottom-dwelling walking forms and burrowers, and rather freely swimming individuals. From the branchiopods, known as fossils first from the Cambrian, probably arose the rest of the crustaceans. These, as exemplified in the living Apus, approximate the hypothetical ancestral crustacean, and, except for the carapace shell fold and the stalked eyes, are very similar to trilobites. Barnacles probably arose from the ostracods, with the adoption of a sessile mode of life.

The clear correspondence of body segment for body segment and appendage for appendage in the eurypterids, limulids, and scorpions, indicates a close genetic relationship (See p. 365). They probably represent three offshoots from a single group that arose from the primitive arthropod stock during the Proterozoic. From this stock, too, descended the remaining arachnids — the tracheate air-breathers.

The evolution of the insects is still imperfectly known. They agree closely with the centipedes (chilopods) of the Myriapoda and with the crustaceans in the segmentation of the head region. The compound eye of insects and of crustaceans resemble each other too closely to be imagined as arising independently in the two groups. The most primitive of living insects are usually considered to be the bristle-tails (Thysanura). The Orthoptera are the most primitive living winged insects and, according to one hypothesis, were derived rather directly from an early group of the Thysanura. The various ground plans represented by the insect orders radiated in many directions, as the Orthoptera into the cursorial group (cockroach and praying-mantis) and the saltatorial (grasshopper and cricket).

Tracheæ have apparently arisen independently in the arachnids, the isopod crustaceans, the Onychophora, the insects, and probably at least twice among the members of the composite class Myriapoda.

Arthropods as Rock-Builders

Not one of the various classes of arthropods is an important aid in the upbuilding of strata. The skeleton of chitin is very thin as compared with the lime skeletons of corals, echinoderms, molluscoids, and mollusks. Arthropods, moreover, live in areas where much sediment mixes with the cast-off skeleton. At times they are very numerous in shales or limestones. Of the various arthropod groups, ostracods and trilobites are of most importance in rock formation. Among the ostracods, Leperditia is very abundant in the late Silurian and early Devonian strata of the Appalachian region. The early Devonian (Helderbergian) strata of the same region are at times charged with the trilobite genus Dalmanites, and the mid-Cambrian Stephen formation in British Columbia is strewn with various genera of trilobites.

1. Divide the phylum into classes and minor subdivisions, giving an example of each.
2. What characters distinguish the Arthropoda from other phyla?

3. Give some characters which place them at the top of all invertebrate animals.

4. How long geologically has this phylum been in existence?

5. How do you account for the earlier existence of water-dwelling than of air-dwelling arthropods?

6. Define Arthropoda, illustrating your definition with examples.

7. How do the Arthropoda differ from the Annelida in the following characters: (*a*) habitat, (*b*) protecting and supporting skeleton, (*c*) locomotion, (*d*) food, (*e*) its capture, (*f*) its intake, (*g*) digestion, (*h*) blood circulation, (*i*) excretion of waste, (*j*) respiration, (*k*) nervous system, (*l*) sense organs, (*m*) reproduction, (*n*) geologic range.

8. How do the members of the larger divisions of this phylum avoid competition in food getting?

9. Briefly outline the evolution of the Arthropoda.

10. Discuss arthropods as rock-builders.

CHAPTER XIV

PHYLUM XIII. CHORDATA

In the phylum Chordata, life has an instrument through which it not only can take cognizance of its environment through the special organs of touch, taste, smell, hearing, and sight, but has a centrally controlled system of nerves and a complex muscular system to respond quickly and accurately to this environment. The members of this phylum, comprising the most highly evolved animals, possess in common throughout life or only in the young, (1) the notochord (primitive backbone), a cord of cells developed from the endoderm, extending along the middle line of the dorsal side of the body between the digestive canal and the extension of the central nervous system (spinal cord of higher forms); (2) branchial clefts, a series of clefts perforating the walls of the pharynx; and (3) the neurocœle, one or more cavities within the central (dorsal) nervous system.

The main advance of the typical Chordata (Vertebrata) upon the Invertebrata lies in the development of the second body cavity, which lodges the central nervous system — the spinal cord and its anterior enlargement, the brain. This cavity is dorsal to the one containing the digestive canal, heart, and lungs.

Derivation of name. — Chordata > Latin *chorda,* a cord, referring to the universal presence of the notochord at some stage in development.

This phylum is divided into the following subphyla:

1. Enteropneusta (Adelochorda)
2. Tunicata (Urochorda)
3. Cephalochorda
4. Vertebrata.

SUBPHYLUM 1. ENTEROPNEUSTA (*ADELOCHORDA*)

This comprises but twelve genera, the best-known of which, Balanoglossus, burrows in the sand or mud of the sea-bottom. This mud it passes through its body for the nutriment in it, as do earthworms. In this form the mouth is at one end of the body and the anal opening at the opposite end; paired gill-slits are present; immediately dorsal to the mouth is a small, cord-like body correlated with the notochord of the typical Chordata. This somewhat concealed relationship to the Chordata suggested the name from Greek *adelos*, not manifest, + *chorde*, a cord. (Enteropneusta (Greek *enteron*, intestine, + *pneuma*, breath; the gill-slits open into the anterior part of the alimentary canal.) These forms show relationship also to the annelids and to the Echinodermata. Unknown in the fossil state.

SUBPHYLUM 2. TUNICATA (*UROCHORDA*)

Tunicates breathe by means of gills. The tadpole-like embryo has a well-developed notochord which is confined to the tail region (whence the name from Greek *oura*, a tail, + *chorde*, a cord). The adult body is inclosed in a tunic, suggesting the name Tunicata.

The tunicates are degenerate Chordata. In all but one small order the tail with its included notochord disappears in the adult, which is free-swimming (*e.g.*, Doliolum) or sessile (*e.g.*, the majority of ascidians or sea-squirts). Many in both of these groups form colonies by budding, a process of growth characteristic of plants and of many of the lower classes of invertebrates, but absent in all higher invertebrates and in all the Chordata except these degenerate forms. Most of the ascidians also show degeneration in the development of cellulose within the skin. Unknown in the fossil state.

SUBPHYLUM 3. CEPHALOCHORDA

Notochord extending from end to end of the body, persistent throughout life. Brain slightly developed. No heart present; blood colorless.

The best known species, Amphioxus (the lancelet), is worldwide in its distribution. It is usually about two inches long, tapering at both ends. On each side of the laterally compressed body run powerful longitudinal muscles which are divided into V-shaped segments, the myotomes.

1. Why are the three subphyla — Enteropneusta, Tunicata, Cephalochorda — placed in the Chordata? Give an example of each.
2. What is the significance of the subphyla names and of Chordata?

SUBPHYLUM 4. VERTEBRATA

The notochord extends through the greater part of the elongated body and persists throughout life or gives place to a jointed vertebral column or backbone (whence the name from Latin *vertebra*, a joint of the backbone). The backbone in lower forms consists mainly of cartilage, in the higher forms this cartilage is replaced by bone. The central nervous system (spinal cord) is penetrated by a very small longitudinal canal. The pharynx is perforated throughout life or only in the embryo by paired branchial openings, the gill-slits. The mouth is ventral and anterior, the anus ventral and posterior. An important digestive gland, the liver, is developed as a hollow outpushing of the intestine; the blood from the intestine passes through this before entering the general body circulation. Brain highly developed; a pair of very complex eyes present; heart of three or four chambers; blood with red corpuscles. Paired limbs usually present.

The Vertebrata are divided into the following classes:

Type of the Vertebrata, *Felis domestica* (Figs. 170–173). The cat is a four-footed mammal with the protective skin largely covered with soft hair and with an internal supporting skeleton of bone. Its organs of offense and defense are sharp carnivorous teeth and curved claws.

The elastic skin, which is united to the underlying flesh by a connective tissue, is composed of a deeper layer, the dermis, or corium, and an outer layer, the epidermis. As the superficial cells of the latter are continually drying up and falling off, new cells form beneath. The claws and hair are special modifications of the epidermis. The oil-glands, the product of which keeps the surface of the skin and the hair soft, are developed in the dermis, and each usually opens into a hair follicle — a sac-like sheath lodging the base of the hair. The sweat-glands, whose function is in some mammals to aid in the maintenance of a uniform body temperature, are in the deepest part of the dermis, or even in the tissue beneath, with openings at the surface. They are of comparatively slight importance in the Carnivora, the order to which the cat belongs.

Skeleton. — The cat's body is supported by an internal framework of bone and moved by muscles attached to their outer surfaces. There are about 230 separate bones; these are fewer in the old than in the young, owing to the union of some bones later in life. *Bone* is composed of about one-third organic matter (gelatine and blood-vessels) and two-thirds inorganic matter (lime-phosphate about fifty and lime-carbonate ten per cent). Each bone is covered completely, except on its articulating surfaces, with a membrane, the periosteum; this helps to renew the bone when injured.

The principal portion of the skeleton is the backbone; to it are attached either directly or indirectly all the other bones of the body (see Fig. 170). To it anteriorly is attached the skull — the brain-inclosing box, to which the upper jaw (maxilla) is solidly joined in front and the lower jaw (mandible) attached by muscles and ligaments below, while posteriorly are attached the hyoid bones, which support the larynx, or voice

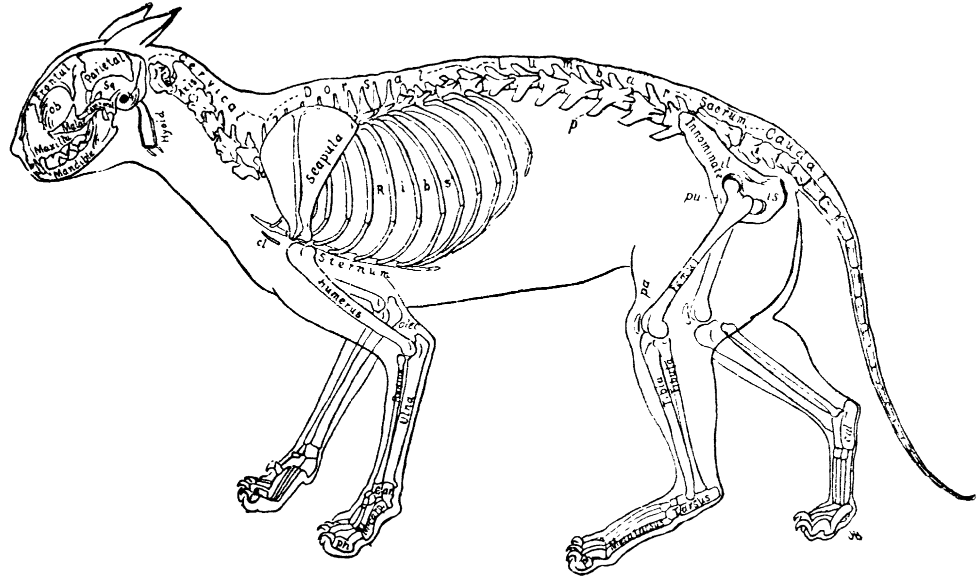


FIG. 170. — The cat, *Felis domestica*, showing the bony framework of the animal; this figure not only gives a good idea of the bony skeleton of all mammals, including man, but in its broader outlines is characteristic of all vertebrates. *b*, basihyoid bone; *cal.*, calcaneum; *car.*, carpal (wrist) bones; *cl.*, clavicle; *il.*, ilium; *is.*, ischium; *m.carp.*, metacarpals; *ob.*, orbit of eye; *olec.*, olecranon process of ulna; *p*, transverse processes of vertebræ; *pa.*, patella or knee-cap; *ph.*, phalanges (toes); *pu.*, pubis; *sq.*, squamosal bone. Reduced in size.

box. To the backbone ventrally are joined the ribs, which with the breastbone (sternum) protect the heart and lungs.

Primitively, as in most fish (Fig. 179) and snakes, a pair of ribs is attached to each vertebra from the base of the head into the tail region. But with upright land life they have become reduced to a small part of the trunk region. Even in the higher mammals, however, there occur in the embryo beginnings of the other ribs which later coalesce with the vertebræ.

The *backbone*, or vertebral column, is a hollow rod lodging the spinal cord, and divided into some thirty to fifty sections, or vertebræ; *i.e.*, seven neck (cervical, Fig. 171), thirteen chest (thoracic), with attachment for the thirteen pairs of ribs, seven back (lumbar), three hip (sacral), and four (in the manx cat) to twenty-six tail (caudal) vertebræ.

In most mammals the number of cervical vertebræ is seven; the long neck of the giraffe has thus been produced merely through the lengthening of the individual vertebræ. With the swan, among the birds, however, there has been an increase in their number to twenty-three and with this a consequent increase in grace of movement.

The *fore limb*, attached to the backbone by muscles only, is composed of

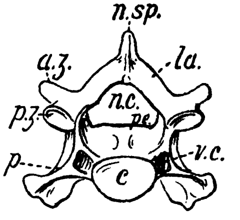


FIG. 171. — Posterior view of the fifth cervical *vertebra* of the cat; to illustrate nomenclature. *a.z.*, anterior zygapophysis, — a flattened articulating surface upon the *neural arch* (*pe.* and *la.* combined), looking downwards upon the posterior zygapophysis of the vertebra ahead. This *a.z.* at times, especially in the lumbar region, looks inwards; *c*, centrum; *la.*, lamina, — transverse portion of the neural arch. Its anterior and posterior faces, called zygapophyses, are flattened for articulation with neighboring vertebræ; *n.c.*, *neural canal*, lodging the spinal cord; *n.sp.*, neural spine; *p*, transverse process, sometimes divided into a superior and an inferior branch; *pe.*, pedicle, — the vertical portion of the neural arch, notched upon the side for exit of nerves from the spinal cord; *p.z.*, posterior zygapophysis; this looks downward (in the lumbar region often outward); *v.c.*, vertebrarterial canal, piercing the base of the transverse process. In the caudal region, especially where the tail is well developed, paired bones, uniting at times to form an arch, arise upon the ventral side of the centrum; these are the *chevron* bones. (Redrawn from Mivart.)

a shoulder-blade (scapula), collar-bone (clavicle), arm-bone (humerus), bones of forearm (radius and ulna), seven wrist bones (carpals) arranged in two rows, five palm bones (metacarpals), and fourteen finger bones (phalanges) arranged in five toes (Fig. 172, *A*). The *hind limb* is composed of the hip bone or innominate, firmly attached to the sacral vertebræ, and made up of the ilium, ischium, and os pubis, the thigh-bone (femur) with the knee-cap (patella) protecting its lower edge, the bones of the foreleg (tibia and fibula), the seven ankle bones (tarsals) arranged in two rows, five metatarsals, and twelve phalanges (three to each of the four toes) (Fig. 172, *B*).

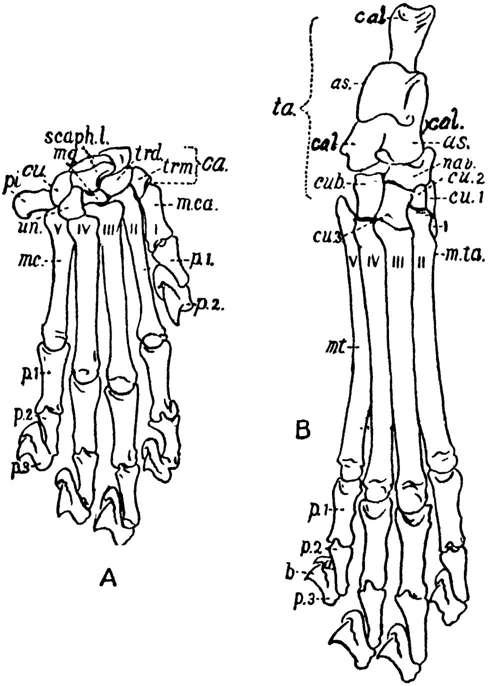


FIG. 172. — *A*, bones of the right *fore foot* of the cat; dorsal view. *ca.*, carpus (or wrist); *cu.*, cuneiform; *mg.*, magnum; *mc.* and *m.ca.*, metacarpal (palm) bones; *p*, phalanges (or bones of the toes); *pi.*, pisiform; *scaph.l.*, scapholunar; *trd.*, trapezoid; *trm.*, trapezium; *un.*, unciform; *I*, *II*, etc., digits, 1st (thumb), 2d, etc. *B*, bones of the right *hind foot* of the cat; dorsal view. *a*, hood to inclose root of claw; *as.*, astragalus; *b*, process to sustain the claw; *cal.*, calcaneum; *cu.1*, *cu.2*, *cu.3*, internal, middle and external cuneiform respectively; *cub.*, cuboides; *mt.* and *m.ta.*, metatarsals; *nav.*, navicular; *p*, phalanges; *ta.*, tarsus (or ankle); *I*, *II*, etc., digits, 1st (represented only by a degenerate metatarsal), 2d, etc. (Redrawn from Mivart.)

The clavicle is vestigial in the Carnivora and entirely wanting in many of the Ungulata. In those vertebrates, however, in which the fore limbs are capable

of a great variety of motions and a freedom of movement, as in flying birds, bats, and in primates, it is well developed.

Hind limbs are wanting among the Sirenia and Cetacea, though a small, degenerate, functionless hip bone is present. In Halitherium, a Miocene sirenian, a vestigial femur is present. In the snakes both fore and hind limbs are absent; but a few forms, as Python, have a vestigial hip bone.

The primitive number of digits to each foot is five, but a reduction occurs in many animals. In the birds there are usually but three upon the wing and four upon the foot; in many reptiles the number is reduced to three; among the mammals the pig has four digits, the rhinoceros three, the camel two, and the horse but one.

The source of the *footprints* made by the pads and claws of the cat's feet in walking upon a yielding surface, such as dense mud, is rather easily recognizable; so, too, that of other living animals. By being covered with sediment these footprints may be preserved fossil. Many such vertebrate fossils occur from the Mississippian to the present. The Triassic sandstone of the Connecticut River valley contains especially notable examples. These footprints made upon an ancient mud-flat are mostly due to the reptiles of the time.

The bones of the fore limbs are attached to the thin triangular scapula, the head of the humerus fitting into a socket in the lower end of this bone, while the hind limbs are similarly attached to the innominate, the head of the femur fitting into a socket in this bone. Both are thus ball-and-socket joints, while the elbow and knee, at the junction of humerus and radius, femur and tibia respectively, are hinge joints.

Joints. — The articulating surfaces of bones at immovable joints, as between the bones of the skull, are separated by a fibrous membrane only, hence the contiguous bone surfaces are irregular and they are stronger thus than when smooth. At joints where there is very slight movement, as between contiguous vertebræ, each surface is faced with a layer of cartilage and the bone surface is but slightly rough. At joints where movement is very free, as the ball-and-socket and the hinge joints, the bordering surfaces are also covered with cartilage, but the two bones are likewise held apart by a fluid; the bone surfaces here are very smooth. Hence in fossil bones the place and extent of movement between bone surfaces is easily noted.

Muscles. — The complicated muscular apparatus, by which the various parts of the body are moved, is primarily derived from the vertical muscle segments (myomeres) lying on each side of the spinal column (as seen typically in Amphioxus and the fish). But in the cat, as in all forms above the fish, this arrangement is obscured, since the muscles are greatly modified both in form and position in adaptation to terrestrial life. The muscles, commonly called flesh, are made up of fibers (coarsest in fish), which are bound together into bundles. These bundles, or true muscles, are usually fastened by each end to a roughened surface of a bone by means of the tough membrane of the periosteum, the larger the muscle the larger being the roughened surface or projection for attachment. Since muscles make up the bulk of the cat's body, the muscular system largely determines the shape of its trunk and limbs (see page 25).

More than four hundred of the muscles found in the cat's body occur also in man with the same general location, function, and nerve supply.

All muscles are either voluntary, under control of the will, or involuntary. The voluntary muscles, all muscles moving the bones, for example, are supplied with nerves from the brain or spinal cord. The involuntary muscles, such as those in the walls of the blood-vessels and digestive canal, are supplied with nerves from the sympathetic nervous system.

The interior of the trunk, called the body cavity, is divided into two parts by a flat partition-like muscle, the *diaphragm*, attached to the backbone and ribs (Fig. 173, *di.*). The anterior or thoracic cavity contains the heart and lungs; the posterior or abdominal cavity contains the stomach, intestine, liver, and kidneys.

Digestion. — In a wild state the food of the cat consists principally of animals which it procures by means of its sharp claws and sharp teeth. This is then partially crushed by the teeth and at the same time preparatory to being swallowed is thoroughly moistened by the saliva. Passing down the œsophagus the food enters the stomach, where the gastric juice dis-

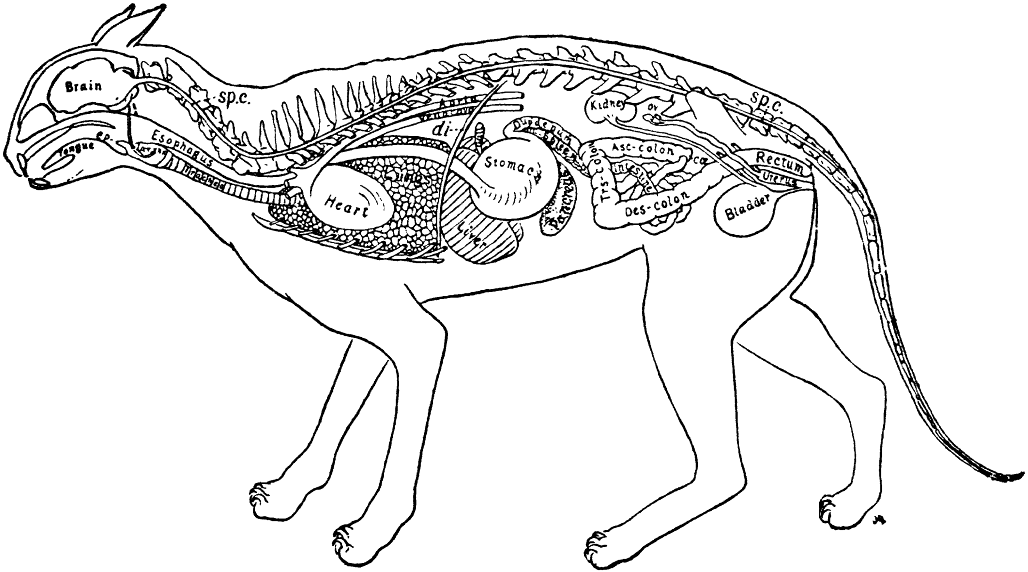


FIG. 173. — The cat, *Felis domestica*, showing the principal internal organs. *Aorta*, the artery carrying the purified blood to all parts of the body; *asc.*, ascending; *cæ.*, cæcum, the blind pouch formed at the end of the colon, where the small intestine enters it (in the cat this cæcum does not end in a vermiform appendix as it does in man and some other animals); *des.*, descending; *di.*, diaphragm, a muscular partition completely separating the abdominal and thoracic cavities; *ep.*, epiglottis (when food is taken, this triangular valve closes the larynx and the food passes over it into the œsophagus); *ov.*, ovary; *sp.c.*, spinal cord; *trs.*, transverse; *vena cava*, the vein returning the impure blood from the body to the heart to be pumped to the lungs for purification. Reduced in size.

solves the proteid constituents, thence to the small intestine, where bile, poured in from the liver, emulsifies the fats, and the pancreatic juice from the pancreas acts upon starches, proteids, and fats. The digested food is absorbed by the many blood-vessels and lymphatics surrounding the digestive canal, especially the stomach and small intestine; the undigested remnant passes through the large intestine and out by the anus.

As in most of the higher animals, both Invertebrata and Vertebrata, the digestive canal is much coiled so that there is a greater area for digestion and absorption; in the cat it is five times the length of the body exclusive of the tail.

The cat has two sets of *teeth;* the thirty of the second or permanent set begin to displace the twenty-six of the first set or milk teeth at the end of the fourth month. In the adult cat there are in the upper jaw, upon each side, three small cutting teeth or incisors, one fang or canine, three premolars, and one molar. The back premolar, very large and especially adapted to cutting flesh, is called the *sectorial* tooth. In the lower jaw, each side has three incisors, one canine, two premolars, and one molar, the molar being the sectorial tooth here. Sectorial teeth are characteristic of the Carnivora.

In the elephant the single pair of upper incisors develop into tusks. Mammals that chew the cud, like the sheep and cow, have no upper incisors in the adult state, though they are present in the embryo, and in their Tertiary precursors they were well developed.

Absorption and blood circulation. — As the food is absorbed from the digestive canal, the (1) emulsified fats and most of the water are carried immediately to the heart and are thence forced to all parts of the body, where the former are stored in the fat-tissue, the (2) sugars, including what when eaten was starch, are taken to the liver, where they are stored until needed; the (3) proteids are taken directly to the liver, where their preparation for use in the body is continued. The energy and heat of the food is set free in the millions of body cells through oxidation, the oxygen being derived from respiration. The end products of (1) and (2) are carbon dioxide and water, in (3) there exist in addition mainly such waste products as urea and uric acid.

This nutrient food, added to the blood already existing, is

pumped by the very muscular heart to all parts of the body through a system of contractile, non-collapsible tubes, the arteries; these keep branching until every portion of the body is reached, and are so numerous that the point of a needle cannot penetrate the body without piercing one or more of them. As the terminal microscopic tubes, called capillaries, are exceedingly thin and delicate, the food material and oxygen pass through the walls, partially at least by osmosis, into the cells needing them, while back into the tubes pass the waste products of the cells, such as carbonic acid and nitrogenous compounds. The blood, now laden with waste material, passes backwards towards the heart through a system of collapsible tubes, the veins; some of the blood is carried through the kidneys, there getting rid of the waste products from the breaking down of the proteids; the inorganic salts and much water are likewise brought to the kidneys. From the heart it is all pumped to the lungs, where much of the carbon dioxide is given up by the blood and oxygen is taken into it.

Body waste. — Thus the solid waste passes out of the body by way of the digestive canal; the liquid waste by means of the kidneys through the bladder, and also through the agency of the sweat glands; the gaseous, through the lungs.

Respiration is performed by the *lungs*, a hollow, blind, spongy outpushing from a part of the throat (pharynx). Air is drawn into and forced out of these, through nasal passages, pharynx, larynx, and trachea, by the contraction and relaxation of the muscles of the chest. Since a network of blood capillaries lines each of the myriad of minute air-chambers, the interchange of carbon dioxide and oxygen is rapid. The oxygen carrier of the blood is the hemoglobin of the red blood corpuscles, for which oxygen has a strong affinity.

Voice. — An outgrowth of this method of respiration is the development of voice. As the air passes to or from the lungs it must traverse the larynx (Fig. 173), upon the sides of which are developed folds — the vocal cords; the rapid passage of the air over these produces an audible vibration. As muscles are at-

tached to the ends of these, they can be expanded and contracted, thus giving rise to variations in the pitch of the voice.

Nervous systems. — The nervous elements form (1) the *central* nervous system, and (2) the *peripheral* nervous system. The former consists of the brain and spinal cord; the latter is made up of those nerves which establish a connection between the periphery of the body and this central system. The *brain*, situated in the posterior portion of the skull, gives off, especially to the muscles of the head and neck, twelve pairs of cranial nerves. The *spinal cord*, which is continuous with the brain and occupies a tube extending through the spinal column, gives off, especially to the muscles of the legs and trunk, forty pairs of spinal nerves. The cranial and spinal nerves with the nerves of the sympathetic system and their associated ganglia constitute the *peripheral nervous system*. The *sympathetic* nervous system, a derivative of the spinal nerves, consists of a pair of nerve-cords extending from the base of the skull to the root of the tail, one upon each side of, and ventral to, the backbone. From these, branches are given off especially to the blood-vessels and digestive system. At intervals throughout the entire system are enlargements, or ganglia, from which additional nerves arise. The peripheral nerves, composed of fibers of various kinds, divide and subdivide until they reach every minute portion of the body. The spinal cord and the sympathetic system are in communication by means of nerves passing from the ganglia of the main sympathetic nerve-cords to the ventral branches of the spinal nerves.

Organs of special sense. — The vertebrate *eye* is the most highly developed eye in the animal kingdom. It consists of a more or less globular body protected by a tough, fibrous outer layer, the sclerotic coat. Through the anterior transparent portion of this, the cornea, the light passes; next it passes through a watery fluid, the aqueous humor, then through the central black spot, the pupil. The bi-convex tissue forming the lens next concentrates the rays in an image which is projected back through the jelly-like substance, the vitreous humor,

upon the inner coat of the eyeball, the retina. In the retina are lodged the ends of the nerves of sight; these take the sensation, transmitting it to the brain, where the image is perceived. The middle coat of the eye is lined with black, which absorbs all deflected light rays, hence the colorless pupil appears to be black. The colored portion surrounding the pupil, the iris, contains numerous radial and circular muscle fibers, by the contraction of which alternately the pupil is enlarged and reduced in size, for times of less and greater amount of light respectively. The lens is inclosed in an elastic sac and by means of muscles fastened to the sides of the eyeball may be decreased or increased in convexity for seeing objects at a greater or less distance respectively. The eyeball is kept distended by the large mass of vitreous humor and by the smaller aqueous humor.

In vertebrates below the mammals, and even in the Monotremata, the sclerotic coat is more or less cartilaginous, and within it many species have developed a ring of delicate, bony *plates* near the junction with the cornea; these *sclerotic* plates surrounding the orbit of the eye are especially conspicuous in the extinct Stegocephalia and Ichthyosauria, in lizards, chelonians, and modern birds. (Fig. 185, *scl.*)

The organ of *hearing* is similarly a complicated apparatus. As in the invertebrates it acts likewise in the maintenance of equilibrium, though in the more highly organized vertebrate only a portion of the hearing mechanism, the semi-circular canals, performs this function. The sense of *smell* is lodged in the nasal cavity, that of *taste* chiefly in the tongue, while the surface of the entire body is an organ of *touch*.

Cats are of two **sexes**. The ova are fertilized within the female by the spermatozoa introduced by the male. Soon each developing embryo, the fœtus, becomes attached to the walls of the uterus by a special structure, the placenta. Through this it is nourished for fifty-five or fifty-six days. The young are then produced, usually five or six at a birth, fully formed except that the eyelids are still closed and the hairy covering is incomplete. The young before birth are enveloped in several fœtal membranes. The inner one, called the amnion, is similar

in the reptiles and birds. Because of its presence in the three groups, the reptiles, birds, and mammals are sometimes classed together as the *Amniota*. After birth the young of the cat are nourished by milk, which is secreted by skin glands known as breasts or mammæ. Because of the possession of these glands the group of animals to which the cat belongs is called Mammalia.

1. Examine the mounted skeleton, identifying the various bones by means of the illustration and description.
2. How is the cat protected against changes in climate? from enemies?
3. Compare in general the composition of a bone with that of a clam or oyster shell.
4. Give two causes of variation in the total number of bones in the cat.
5. Compare the arrangement of the ribs in the cat with that in fish and snakes.
6. What evidence does the cat show in its development that its ancestors possessed a larger number of ribs?
7. Compare the elongation of the neck of the giraffe with that of the swan.
8. How are the fore limbs attached to the trunk? the hind limbs?
9. In what groups of vertebrates is the clavicle well developed? In what vestigial or entirely wanting? Account for this difference.
10. What does the condition of the clavicle in the cat indicate as to its past history?
11. Of what significance are the vestigial hip bones in the Sirenia and Cetacea?
12. What is the primitive number of digits in a mammal? Note variations from this.
13. What is the function of joints? How can you note their presence in fossils?
14. Distinguish between voluntary and involuntary muscles. Give examples of each.
15. Given the bones of an extinct vertebrate, how can you estimate its shape when living?
16. Describe briefly the digestion and assimilation of the cat's food from its capture to its use by the millions of individual cells.
17. Enumerate the cat's teeth with the special function of each group. What special tooth distinguishes the Carnivora, both recent and fossil?
18. How many sets of teeth does a cat have?

19. Give an example of change of function in teeth; of reduction in numbers.
20. Describe briefly the course of the blood through the circulatory system.
21. What element is necessary to the freeing of the energy and heat stored up in the food?
22. Describe the procurement of oxygen by the living body.
23. How is voice produced?
24. What is the source of the bodily waste and how is it excreted?
25. What coördinates the various parts of a muscle, or the different muscles or organs, so that they work together?
26. Describe briefly the central nervous system; the peripheral system.
27. What in general would be the path of a nerve impulse passing from the intestine to the brain?
28. Describe the passage of light from its entrance into the eye of a vertebrate to its perception by the brain.
29. What are sclerotic plates? Where developed and in what animals?
30. Besides sight, what other senses does a cat possess? Where is each located?
31. What is meant by the Amniota?
32. How are cats nourished before birth? How after birth?
33. Why are cats called mammals?

CLASS A. OSTRACODERMI

Bilaterally symmetrical, with persistent notochord and endoskeleton not usually calcified. Movement accomplished by lateral undulations of the body. Jaws very primitive, and only pectoral paired fins present. Head inclosed in a small brain case that contained three pairs of sense organs, corresponding to the olfactory, optic, and otic (ear) capsules of higher vertebrates and equipped with cranial nerves. Beneath the brain case was a large chamber containing the mouth cavity and the gill pouches, these features all closely paralleled in the larvæ of living lampreys. Ostracoderms are known from the Ordovician to the Devonian inclusive.

The class includes the Pteraspida, Anaspida, and Cephalaspida (Osteostraci). In the last group, Stensiö has shown that the first gill

sac was situated in advance of the position occupied by the jaws in higher vertebrates. It can thus be assumed that the group was without jaws; they probably gave rise to the Cyclostomes. Head and trunk depressed, indicating that these and the Pteraspida were probably bottom-dwellers (Fig. 174).

The Pteraspida (Heterostraci) had depressed head and trunk and short tail, with a heterocercal tail-fin (see p. 401). Mouth was subterminal and eyes small and far apart. There was a single external gill opening. The body was covered with denticles (in the Cœlolepidæ) or with bony plates and scales (in the Pteraspidæ and Drepanaspidæ). Impressions on the under side of the dorsal shield of Cyathaspis show that there was a series of gill sacs, and that the nasal organs were paired but contiguous.

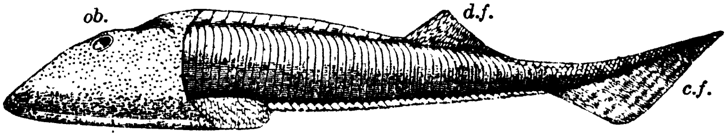


FIG. 174. — Restoration of the ostracoderm, *Cephalaspis murchisoni*, from the Upper Silurian of England. *c.f.*, caudal fin (this is heterocercal); *d.f.*, dorsal fin; *h.s.*, head shield; *ob.*, orbit of eye. (From British Museum Catalog.)

The Anaspida had a normal fish shape, with a series of gill openings on each side, a terminal mouth, and lateral eyes. Examples, Lasanius, Birkenia.

1. Show that the ostracoderms were vertebrates.
2. When did they live?

CLASS B. CYCLOSTOMATA

Degenerate eel-like animals, without ordinary jaws but with a round, sucker-like mouth (whence the name from Greek *cuclos*, a circle, + *stoma*, mouth). Paired fins absent. Gill-slits and notochord are present. From the latter rise rods of cartilage which partially protect the spinal cord above.

It is doubtful if the Cyclostomata are known from the Paleozoic, though Palæospondylus of the Devonian of Scotland, about two inches long with an eel-shaped body, may be a cyclostome.

Existing forms are the lampreys and hagfishes. Lampreys

suck the blood from their prey; hagfishes bore their way into fish and devour their soft parts. The larvæ of the lamprey (Petromyzon) is very different from the adult. Its method of breathing and feeding is like that of Amphioxus and the tunicates; a current of water produced by ciliary action enters the mouth carrying minute organisms which are entangled in a mucous secretion. It agrees with these forms also in the structure of the pharynx, which has a ventral longitudinal groove that secretes a sticky slime.

1. Give distinguishing characters of Class Cyclostomata, also a living and a possible fossil example.
2. What is their probable origin?
3. Show that the larva of the cyclostome lamprey is similar to the adult Amphioxus of the Cephalochorda. What significance has this from the viewpoint of evolution?

CLASS C. PLACODERMATA

Bilaterally symmetrical, with persistent notochord. Head and trunk are inclosed in an armor of bony plates. The animals propelled themselves by a pair of jointed appendages, somewhat like the walking legs of crabs. They had acquired external jaw plates, which were supported internally by cartilaginous bars homologous with the true jaws of sharks. This class had thus passed from jawless to jaw-bearing forms.

The Placodermata (Devonian) are subdivided into the orders: (*a*) Antiarcha, including Bothriolepis, Asterolepis, and Pterichthys; (*b*) Arthrodira, exemplified by Coccosteus and Dinichthys. The latter has at times been found with a head over three feet long by two feet broad.

1. In what respect do the Placodermata represent an advance upon the Cyclostomata?
2. When did they live?

CLASS D. ELASMOBRANCHII

These, the sharks, dogfish, rays, and skates, resemble true fishes (Pisces) in external form but differ widely in structure.

Like true fish they possess paired fins. The internal skeleton is composed essentially of cartilage. The notochord in the adult is surrounded and partially replaced by cartilage which forms the centra of the vertebræ. Processes arise from these and surround the spinal cord. External (dermal) skeleton nearly always present; when present it is of a *placoid* type, that is, each scale consists of a basal plate of bony tissue bearing a pointed spine and composed of dentine covered with enamel. Such skin is called shagreen. Dermal fin-rays are horny. A cloaca is present, serving as the common outlet for the anal, urinary, and genital products. Extending outward from each gill-arch and supporting the gills is a long, broad plate or septum (whence the name from Greek *elasmos*, a plate, + Latin *branchia*, gill). These fishes breathe by opening and closing the mouth instead of only sucking; in this they display a vast advance over the Cyclostomata. The sharks lay few eggs, but each contains much yolk, and hence the embryo is well developed when leaving the shell. The majority of the elasmobranchs are marine, a few genera only living in fresh water.

They differ from the Pisces in lacking membrane bones, air bladder, true scales, gill cover, and ribs.

The Elasmobranchii (Upper Silurian to present) are subdivided into the orders: (*a*) Pleuropterygii (Devonian-Permian), — lateral fins very primitive as shown in the well-known genus, Cladoselache, from the Upper Devonian (Cleveland shale) of Ohio; (*b*) Ichthyotomi (Mississippian-Triassic), best known in the world-wide genus Pleuracanthus; (*c*) Acanthodii (Upper Silurian-Permian), a large Paleozoic group, with the anterior margin of each fin supported by a stout spine, exemplified by Acanthodes; (*d*) Selachii, Devonian to present. Examples of the selachians are: (1) Cestracion, found from the Jurassic to the present, most characteristic of the Mesozoic. This genus shows close relationship to some Pennsylvanian and Permian forms, and survives to-day in the two or three species of Port Jackson shark of Australia, Japan, and California. (2) Lamna and (3) Carcharodon (Fig. 175) (both from Cretaceous to present)

have teeth with a sharp, wedge-shaped crown fixed upon a somewhat bifurcate base which is much compressed antero-posteriorly. The teeth of the former (Lamna) have small lateral denticles at the base of the crown. Here likewise are placed the other existing sharks, dog-fish, and skates. (*e*) Holo-

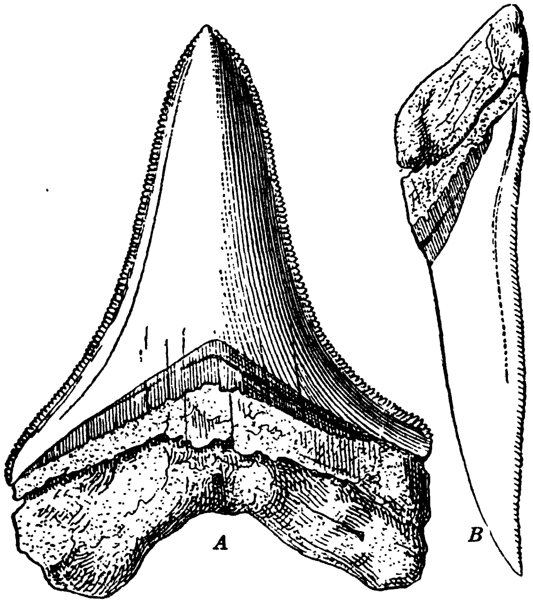


FIG. 175. — Tooth of the extinct marine shark, *Carcharodon megalodon* Charlesworth, from the Miocene (Calvert) of Maryland. Natural size. It is much more abundant in the Eocene of South Carolina. *A*, anterior tooth, inner face. *B*, same in profile. (From Eastman.)

cephali (Jurassic—Recent). An example is Chimæra, widespread in the present seas, called sea-cat in the United States.

1. What distinguishes the class Elasmobranchii?
2. How does it differ from class Pisces?
3. Give its geologic range.
4. Name some living examples of this class. Name some fossil examples.
5. Sketch a tooth of Lamna or Carcharodon, both broad and narrow views.

CLASS E. PISCES (TRUE FISHES)

Cold-blooded, aquatic vertebrates, both marine and fresh water. The organs of locomotion are the paired fins and the flexible tail. *Gills* are the chief, usually the only, organs of respiration, and are attached to the gill arches throughout life. The notochord is more or less completely replaced by cartilaginous or bony vertebræ. (The ancestral development of the notochord is summarized on page 452.) The skull is well developed; in its embryonic growth each of the two bars of the *first* (mandibular) *visceral arch* divides into a dorsal and a ventral portion. The former, the palatoquadrate cartilage, is situated forward and, uniting in the median line with the corresponding portion of the opposite bar, forms the upper jaw. The latter, Meckels cartilage, similarly extends forward and, uniting with its fellow, forms the lower jaw. The *second* (hyoid) *visceral arch* likewise divides into a dorsal and a ventral portion. The latter amongst other uses serves to support the tongue. Most fishes lay *eggs*, but in some forms (*e.g.*, the blenny of the Teleostomi) the young are developed within the mother and brought forth alive; they usually develop lying free within the uterus, but exceptionally are attached to its walls. The eggs, when produced, vary much in size; where they are minute, *i.e.*, with little yolk, they are exceedingly numerous, and where large, few.

Development of fins.— Fishes are conceived to have originally possessed (1) a median fold of skin extending along the back from the base of the head around the tail almost to the anus, giving rise by division to the dorsal, caudal, and anal fins, and (2) a horizontal fold extending from the gills to the tail, giving rise to the paired fins — the pectorals and the ventrals or pelvic fins (Fig. 176). These fin folds, probably developed as balancing organs, were supported by rods of cartilage extending outward from the vertebral arches. Gradually the fins became shortened, the cartilaginous rods supporting them became crowded together though still parallel (as in the Pleuropterygii of the early

Paleozoic); next followed either a fusion of the basal supports of each fin into one (as in the Ichthyotomi of the late Paleozoic, in the Paleozoic and Mesozoic Crossopterygii, and in the living Dipnoi) or the cartilages became rudimentary (as in the Acanthodii of the Paleozoic and the Actinopterygii of Paleozoic time to the present).

Caudal fin. — When the tail fin is divided into two somewhat equal lobes and the vertebral column extends nearly to its end, it is most primitive and is called *diphycercal* (Fig. 176).

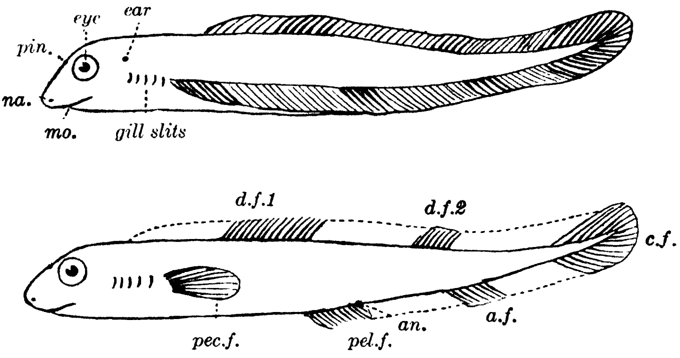


FIG. 176. — Ideal diagram representing the probable development of the fins. *A*, fish with a continuous fin-fold. *B*, fin-fold broken up into distinct fins. *a.f.*, anal fin; *an.*, anus, in position midway between the two pelvic fins; *c.f.*, caudal fin; *d.f.1*, anterior, and *d.f.2*, posterior dorsal fins; *ear*, location of the auditory organ, — the semicircular canals (functioning both in hearing and in the maintenance of equilibrium); *mo.*, mouth; *na.*, nasal opening; *pec.f.*, pectoral fin; *pel.f.*, pelvic or ventral fin; *pin.*, pineal eye; *a.f.*, *d.f.1*, *d.f.2*, and *c.f.* are unpaired fins, while *pec.f.* and *pel.f.* are paired fins.

When the vertebral column extends into the upper lobe, making it much longer than the lower one, the caudal fin is called *heterocercal* (Fig. 174). When, with nearly equal lobes, the column stops near the base of the fin, it has received the name *homocercal* (Fig. 179). In most Paleozoic fishes the caudal fin is diphycercal or heterocercal. From the Cretaceous onward, adult bony fish have usually homocercal tail fins, but they are always diphycercal or heterocercal in the immature stage.

Derivation of name. — Pisces > Latin *piscis,* a fish.

The class Pisces is divided into the following subclasses:

SUBCLASS 1. TELEOSTOMI (BONY FISHES)

In the Teleostomi (Devonian to present) the skull and shoulder girdle have many dermal bones in addition to those of the internal skeleton; many of these dermal bones enter into the formation of the upper and lower jaws (whence the name from Greek *teleos,* complete, + *stoma,* mouth). The entire skeleton is usually more or less ossified. Fin-rays are bony. Gills are covered by an operculum. Anus is distinct from the urinary and genital openings. Tail is homocercal except in such survivors of ancient types as the sturgeon and garpike, in which it is heterocercal. Swim bladder is used merely for hydrostatic purposes, not respiratory.

The Teleostomi are subdivided into the following orders:

Orders 1 to 3, inclusive, often classed as *ganoids,* include few living forms but were exceedingly numerous during Paleozoic and Mesozoic times; their scales are thick, usually rhombic plates composed of a bone-like dentine — ganoin — giving an iridescent appearance, and generally united to one another by peg and socket joint, hence strong and flexible. Orders 2–4 are sometimes classed together as actinopterygians.

Order 1. Crossopterygii (Lobe-finned Ganoids)

In living forms the pectoral fin is made up of a solid basal portion supported by internal bones and a fringe of rays (whence the name from Greek *crossoi,* a fringe, + *pterygion,* a small

wing). In early fossil forms the fins were basically limb-like. The pectoral fin possessed, in proper sequence, the clavicle and scapula, the latter with a cavity into which fits the rounded projection of the humerus, and, attached to the distal end of this, the radius and ulna (Fig. 177). Beyond these are bones which correspond in part to the bones of wrist and fingers. Caudal fin is diphycercal. The air bladder is an accessory respiratory organ.

This is an ancient order, beginning in the Devonian. It combines characters of the Elasmobranchii, Dipnoi, and Tele-

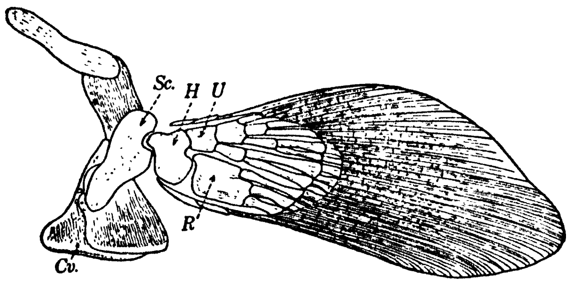


FIG. 177. — Pectoral fin of the crossopterygian fish *Sauripterus taylori*, the lizard-fin from the late Devonian rocks. *Cv.*, clavicle; *H*, humerus; *R*, radius; *Sc.*, scapula; *U*, ulna. (After W. K. Gregory.)

ostomi, and is represented at present by but two living species — Polypterus of the Nile valley and equatorial Africa, and Calamoichthys from western Africa. Holoptychius is a Devonian form widely spread in North America and Europe. In this genus no ossification has been noted in the sheath of the notochord to form vertebræ. In Eusthenopteron such ossification has begun in the anterior portion.

The three remaining orders of the Teleostomi have no basal fleshy lobe to the paired fins.

Order 2. Chondrostei

Caudal fin is heterocercal. This order includes Cheirolepis from the Devonian of North America and Europe, Catopterus

from the Triassic of North America, and the living sturgeons from seas of the northern hemisphere; the latter enter the various rivers of North America, Europe, and Asia.

Order 3. Holostei

Tail is heterocercal or nearly homocercal. (1) Semionotus (Fig. 178), fusiform, with rhombic scales, the dorsal ones forming a crest. Triassic of North America, Europe, and South

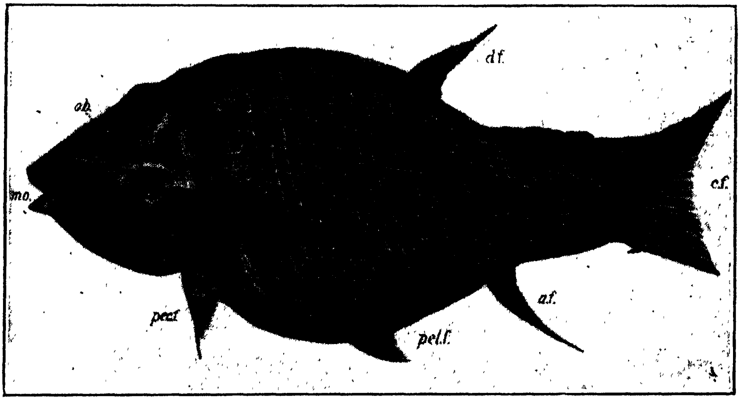


FIG. 178. — An actinopterygian fish, *Semionotus* (*Ischypterus*) *lenticularis* Newberry, from the fresh water Triassic shales of Boonton, New Jersey. *a.f.*, anal fin; *c.f.*, caudal fin; *d.f.*, dorsal fin; *mo.*, mouth; *ob.*, orbit of eye; *pec.f.*, pectoral fin; *pel.f.*, pelvic (or ventral) fin. (Newberry's figure.)

Africa. Those from Massachusetts, Connecticut, and New Jersey were formerly called Ischypterus. (2) The mud-fish (Amia), from the rivers of the United States, and (3) the garpike (Lepidosteus), from the fresh waters of the southern half of North America and Cuba, are living examples; both occur fossil from the Eocene to the present.

Order 4. Teleostei

The teleosts (Jurassic to present) are merely improved ganoids. Scales overlapping, in oblique rows, usually thin,

elastic, generally round with a smooth margin or with the posterior margin toothed. Backbone typically ossified. Tail homo- or diphycercal.

The bulldog fish, Portheus, ten to twelve feet long, was abundant in the Cretaceous seas of North America and Europe. The herrings are known from the Lower Cretaceous to the present; species of Diplomystus (Cretaceous to present) are beautifully preserved in the fresh-water Green River shales (Eocene) of Wyoming, and closely related genera are still living in the rivers of New South Wales and Chili. Of the salmons (Miocene to present), fossil skeletons of the existing *Mallotus*

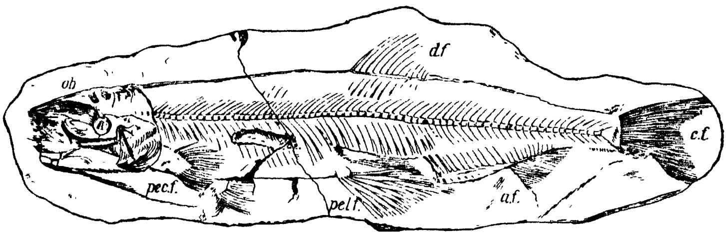


FIG. 179. — The caplin, *Mallotus villosus* Cuvier. (× ⅓.) This member of the smelt family is an abundant fossil in the glacial (Pleistocene) clays of eastern Canada. *a.f.*, anal fin; *c.f.*, caudal fin (this is homocercal); *d.f.*, dorsal fin; *ob.*, orbit of eye; *pec.f.*, pectoral fin; *pel.f.*, pelvic fin. (Redrawn from Logan.)

villosus are very common in concretions in the Pleistocene clays of Greenland and eastern Canada (Fig. 179). The pipe-fishes, catfishes, codfishes, and eels occur from the Eocene to the present, perch since the Cretaceous, and salmon since the Miocene.

SUBCLASS 2. DIPNOI (LUNG-FISH)

Respiration is by both gills and lungs (whence the name from Greek *di*, two, + *pneo*, to breathe; whence, too, the common name of lung-fish; also called mud-fish). In pure water they breathe by means of their gills, like an ordinary fish; but in stagnant or muddy water they come to the surface and draw air into their lungs. The gills are like those of other fishes; the

lung is morphologically the air-bladder of the Teleostomi, but differs in being covered by a network of veins supplied by a special artery, hence acting like a true lung. Notochord persistent without a trace of separate vertebræ except in tail. Cloaca present. Paired fins lobate. Bones mostly cartilaginous.

The Dipnoi (called Dipneusti by some authors) are known from the Devonian to the present. Dipterus and Scaumenacia

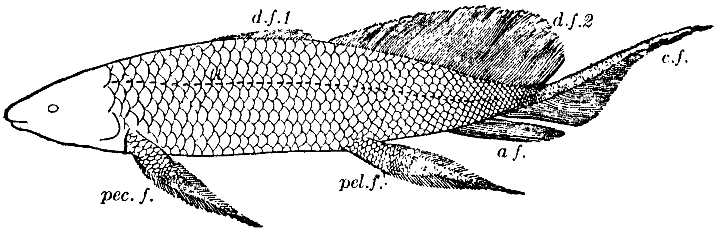


FIG. 180. — A restoration of a dipnoian fish, *Scaumenacia curta* Whiteaves, from the Upper Devonian of Scaumenac Bay, Quebec. *a.f.*, anal fin; *c.f.*, caudal fin (this is heterocercal); *d.f.1* and *d.f.2*, anterior and posterior dorsal fins; *l.l.*, lateral line (a groove lined with sensory hairs); *pec.f.*, pectoral fin; *pel.f.*, pelvic fin. In the last two, — the paired fins, — the flesh of the body extends far into the fin; these fins correspond to the fore and hind limbs of higher vertebrates. Reduced in size. (From Hussakof.)

are well-known Devonian genera (Fig. 180). Ceratodus, spread over the entire world during the Triassic and Jurassic, survives at present only as Neoceratodus in certain rivers of Queensland, Australia, where it lives in quiet pools which become very stagnant during the dry season. The other living forms of Dipnoi are the Lepidosiren of central South America and Protopterus from tropical Africa, both burying themselves in the mud during the dry season.

1. Give distinguishing characters of class Pisces.
2. How do the majority of fish breathe? the lung-fish?
3. State briefly the probable origin of the fins; the three kinds of caudal fin.
4. Define the subclass Dipnoi, noting the significance of the name.
5. Give its geologic range; fossil and living representatives.
6. Give geologic range of the subclass Teleostomi.

7. Into what four orders is this subclass divided? Give fossil and living example of each.

8. Sketch Semionotus in outline, with a small portion of body in detail to show the rhombic scales. Label scale and the various fins. To what order does it belong?

9. Sketch Diplomystus or Mallotus, noting fin-rays, vertebræ. To what order does it belong?

CLASS F. AMPHIBIA

These differ from fish mainly as follows: they have paired five-toed limbs in place of paired fins; each limb consists, as in all the higher vertebrates, of one bone in its upper portion, two in the lower portion, also several wrist or ankle bones and jointed fingers or toes; when a median fin is present, as in the tadpole, it lacks fin-rays. Amphibians breathe by gills in the larval condition, but usually by lungs in the adult. A cloaca is present. Skin usually without scales; it is kept soft by the many mucus-secreting glands, hence the animals breathe also through the skin. The skeleton is ossified. The skull is flat and articulates with the spinal column by two condyles. The ribs are short, not encircling the thorax. Nearly all pass through a gill-breathing, tadpole stage before breathing by lungs. See page 411.

The structure of amphibians is such that they could not adapt themselves to dry air but could live in swamps and damp places where fish could not live. In the order Stegocephalia they tried to adapt themselves to a life upon dry ground but were not very successful.

Derivation of name. — Amphibia > Greek *amphi*, both, + *bios*, life. They are water-dwellers during one portion of their lives, and land-dwellers during another portion.

The Amphibia are divided into the following orders:



FIG. 181 (caption on opposite page).

Order 1. Stegocephalia

Extinct, tailed Amphibia, often very large. There are, as a rule, two pairs of limbs present; usually also a ventral and sometimes a dorsal armor of small, overlapping scales, much like those of ganoid fish. Teeth sharply conical.

These are included with the Amphibia because (1) gill-arches are present in immature skeletons; (2) they breathed by lungs alone in adult, or by lungs and gills; (3) the ribs do not encircle the thorax; (4) the mucus-canal system was well developed as indicated by deep impressions, especially observed in the bones of the head. They show probable derivation from the crossopterygian fishes in that (1) the conical teeth are often complexly infolded (*e.g.*, the labyrinthodonts) as in some Paleozoic fish (*e.g.*, Holoptychius; (2) a ring of bony plates is present around the eye-sockets; (3) a pineal foramen is present; (4) the bones of the skull roof are similar in arrangement.

FIG. 181. — Restoration of a landscape by the side of a sluggish creek in Texas and New Mexico during the Upper Pennsylvanian and Lower Permian times. Of the abundant fauna of this period, about fifty distinct genera of amphibians and reptiles have been recovered. This fauna is of especial interest since it is the oldest known reptilian fauna and the most comprehensive of the older amphibian. Only one example of each is here restored. Upon the land are two figures of Eryops, — a *stegocephalian amphibian*, about seven feet long, with a skull nearly two feet long, while other adult amphibians living with it have a skull no larger than a man's thumb nail. The lowlands must have swarmed with these animals and the contemporaneous reptiles. In the water is a *theromorph reptile*, Limnoscelis, about seven feet long, with a beak-like skull armed with strong conical teeth. Flying above this is one of the giant ancestral "*dragon flies*," Meganeura, some representatives of which had a two-foot spread of wings. The fern-like trees and bushy plants of the foreground are *cycadofilicaleans*. To the right are wide stretches of the huge scouring rush, *Calamites;* on slightly higher ground to the left are *Lepidodendrons* (branched) and *Sigillarias* (unbranched).

One must view this single river bank, creek, or shore of an inlet as a single one of many such landscapes, ever varying in detail. Cordaites, which in later Devonian time made the first great forest constituent of which there is record, is still present, though not shown. So, too, there are hidden in the recesses of the forest the forerunners of the modern coniferous types as well as other forms destined to give rise to the angiosperms. (From Williston, the landscape adapted from Neumayr.)

They lived in fresh water, though some may have been more or less completely terrestrial. In the Joggins coal mines (Pennsylvanian) of Nova Scotia such genera as Dendrerpeton and Hylononmus are common in decayed trunks of Sigillaria and Lepidodendron associated with the fresh-water gastropod *Dendropupa vetusta.* They were abundant in the Texas-New Mexico region during the Upper Pennsylvanian and Lower Permian times (Fig. 181). Primitive groups of the Stegocephalia are probably the ancestors of the other Amphibia and the Cotylosaur reptiles.

Stegocephalia have been recognized from the Upper Devonian to the Triassic. Branchiosaurus is a well-known genus from the Permian and the labyrinthodont genus Mastodonsaurus from the Triassic. The latter is the largest amphibian known, with a skull over four feet long and almost as wide.

Order 2. Urodela (Salamanders)

Tail present throughout life (whence the name from Greek *oura,* a tail, + *delos,* apparent). Two pairs of approximately equal limbs are usually present. In some (as Necturus and the eel-like Siren of North America) gills are present throughout life; in others (as the salamanders and the American Amblystoma) the adult breathes by means of lungs.

Fossil remains are rare. They have been found from the Upper Jurassic to the present. A giant salamander (one meter long) from the Miocene of Oeningen, Baden, was mistaken by the early scientist Scheuchzer for the remains of a man and named by him *Homo diluvii testis* (man as witness of the flood); this famous fossil, now named *Andrias scheuchzeri,* is preserved in the Teyler Museum in Haarlem.

Order 3. Anura (Frogs, Toads)

Tail absent in the adult (whence the name from Greek *a,* implying negation, + *oura,* a tail). Hind limbs much larger than fore. Gills never present in adult.

The eggs of frogs (in shapeless masses) and toads (in ropes) look like little black beads (the yolk) surrounded by transparent jelly (the white). Each bead attracts the sun's rays, which causes the germ or fertilized cell within to develop, through feeding upon the yolk and white, into the embryo young. In about two weeks the embryo leaves what is left of the jelly. It then has external gills; but later internal gills develop from slit-like openings in the gullet walls, and the external gills, always a source of danger, are gradually resorbed. This tadpole is now in the fish stage, in which respiration takes place by the water passing in through the mouth and out through the openings in the gullet walls over the gills. Next the fore and hind limbs bud out and become jointed, lungs are formed, gills and tail are entirely resorbed, and the developing animal becomes adult in appearance.

Fossils are rare, and are known only from the Upper Jurassic to the present. These include remains of both frogs and toads.

Order 4. Gymnophiona

Snake-like, without limbs or tail. The larva has long external gills. Examples are the tropical, subterranean cœcilians, which burrow in moist ground. Fossil remains are unknown.

1. In what ways are the Amphibia an advance upon the fish?
2. Name one way in which the embryo shows its fish ancestry.
3. What is the habitat of the Amphibia?
4. Give the significance of the name.
5. What is the geologic range?
6. Name the four orders into which Amphibia are divided, with a living example of each existing order.
7. Outline the development of a toad.
8. Give an example of the Stegocephalia. Why are these included with the Amphibia?

CLASS G. REPTILIA

Cold-blooded vertebrates, usually with two pairs of five-toed limbs and a horny exoskeleton of scales (*e.g.*, snake, lizard), or of horny (*e.g.*, tortoise) or bony (*e.g.*, Stegosaurus) plates.

Thorax usually near head, hence the short neck. Living reptiles periodically cast off this horny exoskeleton either as a whole or in fragments. They breathe by lungs throughout life. The heart is incompletely four-chambered, the two ventricles being separated by a partial partition. There is no metamorphosis, the young leaving the egg in the adult form; hence the eggs are large. Reptiles are mostly oviparous. The eggs are always laid on land, and are porous for the respiration of the growing embryo. Because of this porosity, the embryo would drown if the eggs were laid in water (true also of birds' eggs). Unlike the Amphibia, the structure of reptiles is such that they could adapt themselves to dry air, and could hence spread more widely upon land.

Reptiles were very abundant and dominant during the entire Mesozoic time; they ruled not only the earth and sea but the air as well.

Derivation of name.— Reptilia > Latin *reptilis*, creeping; from the mode of progression of snakes, the best known of reptiles.

Reptilia are subdivided into the following orders:

Order 1. Cotylosauria

Extinct land reptiles with limbs adapted to the habitual support of the body. Pineal foramen always present. Teeth usually lodged in sockets.

The Cotylosaurs are clearly related to the primitive division of the Stegocephalians, and, like these, lived chiefly in marshes. They were most abundant during the Permian, and have been found from the Lower Permian to the Triassic in North America, Europe, and South Africa. An example is the large, massive Parciasaurus (about ten feet long), with a triangular head, stout limbs, and short tail.

Order 2. Theromorpha

Primitive land reptiles, with limbs usually adapted to the habitual support of the body. Pelvic bones fused as in mammals; the pectoral arch very similar to that of the monotremes (mammals). The many resemblances to the mammals suggested the name, from Greek *ther*, wild beast (mammal), + *morphe*, form. The Theromorphs are thus related both to the mammals and, through the Cotylosaurs, to the amphibian Stegocephalian.

The Theromorpha were well fitted to a land life and radiated into many different families. Their remains are especially abundant in the Karroo formation (Permian and Triassic) of South Africa; they also occur in rocks of similar age in India, Europe, the United States, and Brazil. These include among others the suborders — Pelycosauria (such as Varanosaurus, Casea, and Dimetrodon from the Permian of Texas), Dicynodontia (Anomodontia of authors), and Theriodontia. Included in the last group are the cynodonts, with a tusk-like canine tooth in the upper jaw (*e.g.*, Cynognathus).

Order 3. Ichthyosauria

Extinct aquatic reptiles, with large head, no neck, and a long tail expanded in a vertical plane; they are thus fish-like (whence the name from Greek *ichthys*, a fish, + *pterygia*, fins). The two pairs of limbs are true paddles. They doubtless swam largely beneath the surface of the water, but were compelled to come to the surface for breathing. Within one individual were found the internal skeletons of two hundred belem-

nites; such records as well as the fish scales and bones in the many coprolites left by them indicate that they lived largely upon fish and cephalopods.

These ichthyosaurs, Triassic to Cretaceous in age, parallel the whales amongst the mammals but were smaller, with a maximum length of twenty to thirty feet against sixty to seventy for the whales. Some at least bred their young alive, producing

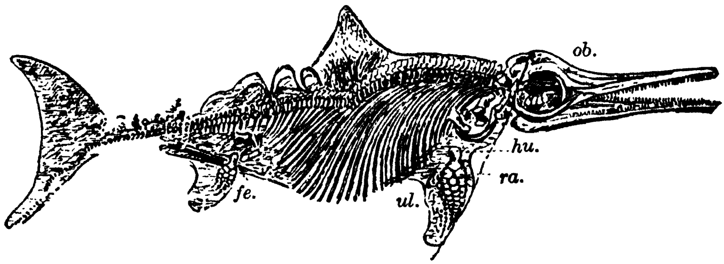


FIG. 182. — The ichthyosaurian reptile, *Ichthyosaurus quadriscissus*, from the Jurassic of Germany. This remarkably preserved form shows not only the outline of the dorsal and caudal fins, but also the integument surrounding the limbs. *fe.*, femur; *hu.*, humerus; *ob.*, orbit of eye; *ra.*, radius; *ul.*, ulna. (After Fraas, from Woodward's "Vertebrate Paleontology.")

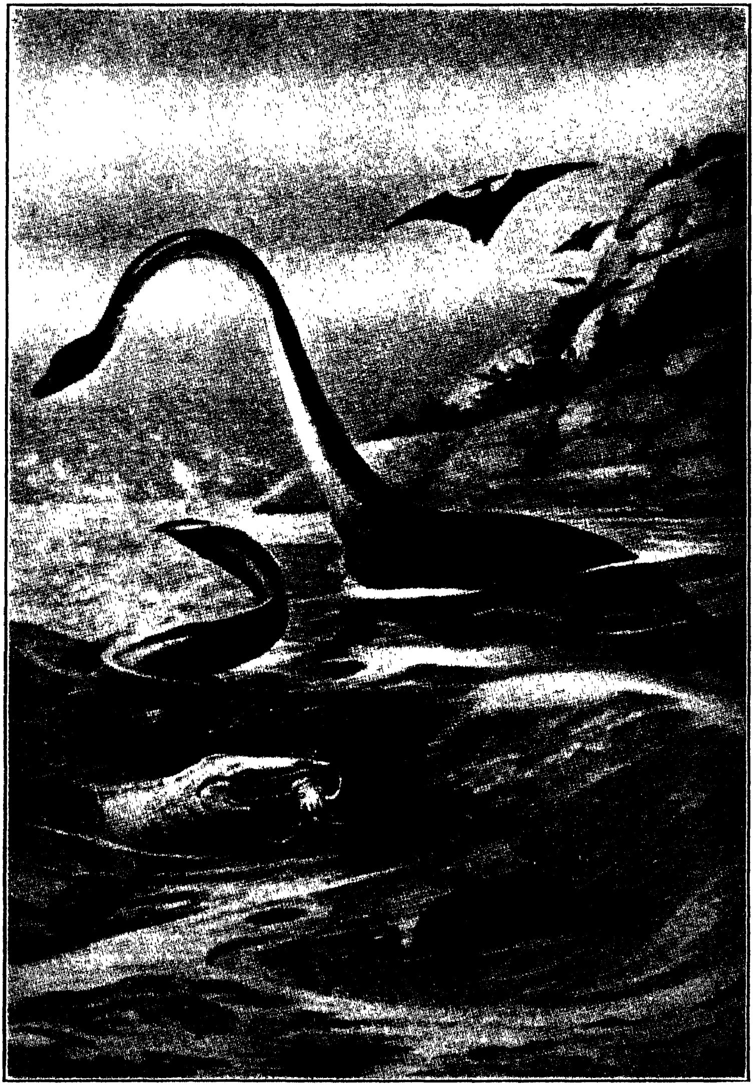
eight to ten at a birth. They indicate, as do the whales, a derivation from land forms; the bones of the forearm (radius and ulna) in the Triassic forms (*e.g.*, Mixosaurus) are always longer and more slender and hence less paddle-shaped than in later forms (*e.g.*, Ichthyosaurus; Jurassic to Cretaceous) (Fig. 182).

Order 4. Placodontia

Primitive amphibious or aquatic reptiles, with dark, pavement-like crushing teeth. Triassic and Liassic of Europe (*e.g.*, Placodus).

Order 5. Sauropterygia (Plesiosaurs)

Extinct, aquatic reptiles (commonly called plesiosaurs), with long neck, small head, and two pairs of limbs; they are



From H. W. Shimer's "Introduction to Earth History," courtesy of Ginn and Company.

FIG. 183. — A probable scene in the Upper Cretaceous sea of North America. The mosasaur Clidastes is catching a squid (Belemnites), the toothed bird Hesperornis is diving for a fish; swimming at the surface is the plesiosaur Elasmosaurus and in the air are flying reptiles (Pteranodon).

thus lizard-like (whence the name from Greek *sauros*, a lizard, + *pterygia*, fins). Teeth conical. A pineal foramen is present. They swam at the surface of the water but could doubtless make swift dives. Some attained a length of forty feet.

Sauropterygians are known from the entire Mesozoic — Triassic to Upper Cretaceous, and from all parts of the world. In Triassic forms (as Lariosaurus) the limbs are long and rather slender, with the normal number of phalanges to the digits, but in later genera (as Plesiosaurus of the Jurassic) the limbs are true paddles with the bones short and the number of phalanges very much increased (Fig. 183). Their ancestors were thus in all probability land animals. Some specimens of Plesiosaurus exhibit what were apparently embryos within the abdomen and hence must have produced their young alive.

Stomach-stones (gastroliths) nearly always accompany complete skeletons of the plesiosaurs, at least those from the Cretaceous of western North America. Within one large specimen from this region were one-half bushel of polished stones, ranging in size up to four inches in diameter. It is known by the bones and shells found in the region of that portion of the body where the stomach must have been located that these plesiosaurs lived upon such invertebrates as Scaphites, and such vertebrates as fish and pterodactyls; they hence probably possessed a gizzard. Evidence is also accumulating to indicate that the stomachs of some dinosaurs, both carnivorous and herbivorous, had a gizzard-like compartment.

Order 6. Chelonia (Turtles, etc.)

Reptiles with body inclosed in bony plates — the dorsal carapace and ventral plastron, composed largely of the expanded dorsal and ventral parts of the ribs. Between these plates the animal can for protection withdraw head, legs, and tail. These plates and often other portions of the body are covered with horny expansions and scales. The jaws are without teeth but are covered with a bird-like horny sheath. (Name > Greek *chelone*, a tortoise.)

Here are included the living tortoises and turtles. Undoubted chelonians are known from the Upper Triassic to the present (Fig. 184).

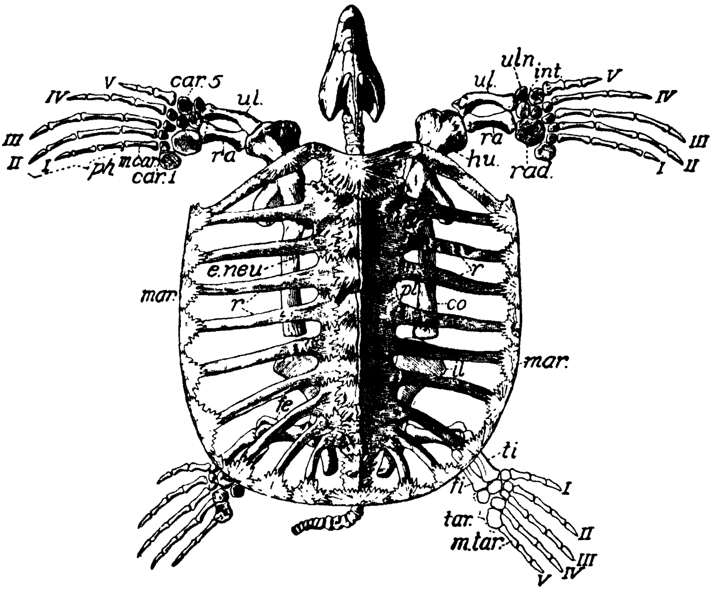


FIG. 184. — The marine turtle, *Archelon ischyros* Wieland, from the Pierre Upper Cretaceous) of South Dakota. Dorsal view ($\times \frac{1}{40}$). The animal was protected (1) dorsally by a *carapace* consisting of marginal plates, ribs, etc., united and covered by leather or horn; (2) ventrally by a *plastron* of dermal bones similarly covered. The jaws have no teeth, but were covered by horn. The distal portion of the right hind limb has been restored; this was bitten off when the animal was young, the end of the tibia and fibula, where the bite occurred, showing healed surfaces. *car. 1 to 5*, carpals 1 to 5, *i.e.*, the distal row of carpal (wrist) bones; *co.*, coracoid; *e.neu.*, epineural plates of the carapace; these dermal plates are usually undeveloped in the Chelonia, only the *neurals* — the expanded processes of the vertebræ — being developed; *int.*, intermedium; *il.*, ilium; *mar.*, the dermal marginal plates of the carapace; *m.car.*, metacarpals; *m.tar.*, metatarsals; *ph.*, phalanges; *pl.*, the dermal pleural (costal) bones, covering only about one-fifth of the length of each rib; *r*, ribs (the anterior one of the ten pairs not showing); *ra.*, radius; *rad.*, radiale; *tar.*, tarsus; *ti.*, tibia; *ul.*, ulna; *uln.*, the ulnare bone of the carpus; *I*, *II*, etc., are the digits, *I* (thumb or great toe), *II*, etc., of the hand and foot, which were distinct paddles. (From Wieland.)

Order 7. Rhynchocephalia

Lizard-like, scaly reptiles with biconcave vertebræ and frequently with a beak at the end of the skull (whence the name from Greek *rhynchos*, a beak, + *cephale*, head).

The Rhynchocephalia are known from the Triassic to the present, with maximum development in the Triassic. The sole survivor is the small Hatteria (or Sphenodon) now living on two or three small islands off the coast of New Zealand. The survival of the very primitive Hatteria is probably primarily due to its removal in the Australian region from competition with the higher mammals, and secondarily to its burrow life, which withdraws it still further from competition.

Order 8. Squamata

Reptiles with an external protection of horny scales (whence the name, from Latin *squamatus*, scaly). The quadrate bone is movably articulated with the skull. Limbs present or absent.

This order, known from the Lower Cretaceous to the present, includes the *lizards* (limbs usually present and adapted for walking), *snakes* (Cretaceous to present, with the long, narrow body devoid of limbs), and *pythonomorphs* (Upper Cretaceous, with a long snake-like body and limbs modified into swimming paddles). The pythonomorphs (or Mosasaurs), (Fig. 183) found all over the world during the Upper Cretaceous, usurped the place left by the declining sauropterygians and ichthyosaurs; Mosasaurus, of North America and Europe, attained a length of fifty feet; Platycarpus (Fig. 185) is abundant in the Upper Cretaceous rocks from Wyoming to Texas.

Order 9. Thecodontia

An extinct, generalized group, somewhat resembling the Rhynchocephalia, from which both the crocodiles and the dinosaurs may have been derived. Permian to Triassic. Examples are Belodon, Ætosaurus, and the creature that made the hand-like footprints, Cheirotherium.

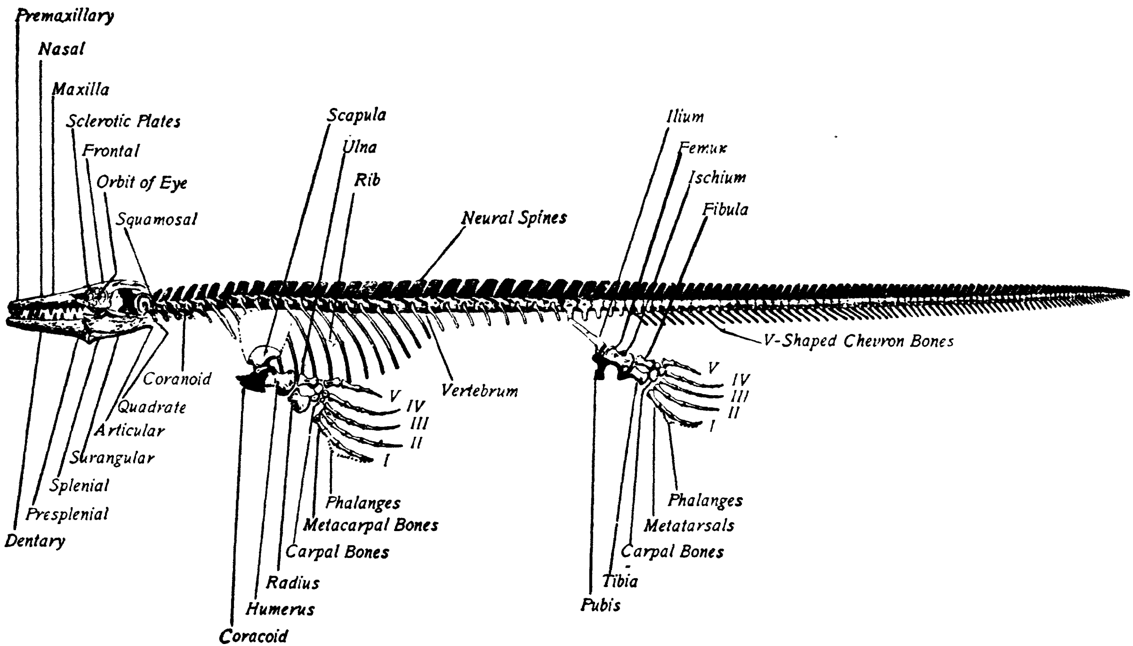


FIG. 185. — The skeleton of a fifteen-foot-long mosasaur, *Platycarpus coryphæus* Cope, from the Cretaceous of Kansas. *I*, *II*, *III*, *IV*, *V*, digits, 1st (corresponding to thumb or great toe), 2d, etc. (Figure from Williston.)

Order 10. Crocodilia

Reptiles with the dorsal surface of body, or both dorsal and ventral surfaces, covered with rows of sculptured bony plates which are covered with horn. Scales also present. Known from the Jurassic to the present.

The Crocodilia are a modern edition of some dinosaur characters. Fossil examples are Teleosaurus and Alligatorium; living examples are the crocodiles and alligators.

Order 11. Dinosauria

Long-tailed, with limbs adapted for habitual support of the body. No pineal foramen. Teeth in sockets or a groove.



FIG. 186. — A nest of eggs of the dinosaur Protoceratops, from Mongolia. The eggs (eight inches long) are seen weathering from the base of a cliff. (Photograph through the courtesy of the American Museum of Natural History.)

Skull usually small in proportion to the rest of the body, and the brain cavity diminutive. The surface of the body was in some forms covered with scales, in others with a bony armor, while in

others it was probably naked. Well-preserved external molds of the skin of various dinosaurs (*e.g.*, Stephanosaurus) have been found in western North America (Fig. 16). Some had sharp carnivorous teeth, others blunt-crowned herbivorous ones. (Name > Greek *deinos*, terrible, + *sauros*, a lizard.) Eggs have been found in France, Mongolia, etc., accompanying the skeletons of both Sauropoda and Orthopoda. In structure these differ from those of living reptiles, and in the thickness of the prismatic layer are more like those of modern birds (Fig. 186).

The dinosaurs are known from the Triassic to the Upper Cretaceous inclusive. They are subdivided into:

A. Saurischia
  Suborder 1. Theropoda
  Suborder 2. Sauropoda
B. Ornithischia
  Suborder 3. Orthopoda.

1. Theropoda. Triassic to Cretaceous. These include forms which were lightly built, walking bird-like upon their toes, with short fore legs and long hind ones, hollow limb bones, sharp carnivorous teeth, and clawed digits. The union of the ischia extended backwards and downwards, forming a kind of third foot when the animal rested upon his hind legs (Fig. 187). One of these, Anchisaurus, has been found only in the Triassic sandstones of the Connecticut valley and is doubtless responsible for many of the three-toed tracks so numerous upon these old muddy sands. Other examples from the Rocky Mountain region are: Ornitholestes, Struthiomimus, and Allosaurus. Theropods varied in length from five to thirty feet.

2. Sauropoda. Jurassic to Cretaceous of North and South America, Europe, Asia, Africa, and Australia. Their dentition, suggesting that they fed on succulent plants, their rather solid limb bones, comparatively weak limb joints, and the character of the strata inclosing the bones, indicate that they lived in swamps and estuaries. In such a habitat their long necks would

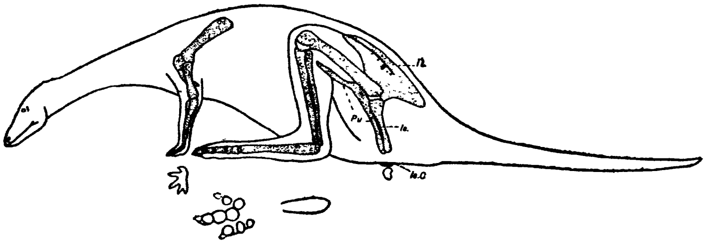


FIG. 187. — A bipedal dinosaur, *Fulicopus lyellianus* Hitchcock, known only from its tracks preserved in the Triassic shaly sandstones of the Connecticut Valley. Here restored in the act of drinking. The bones of the left fore and hind foot are shown in place, and in the foreground their tracks in the mud. Beneath the union of the pubis (*Pu.*) and ischium (*Is.*) a callosity (*Is.C.*) is represented, making the impression in the mud beneath; *Il.* ilium. (After Lull.)

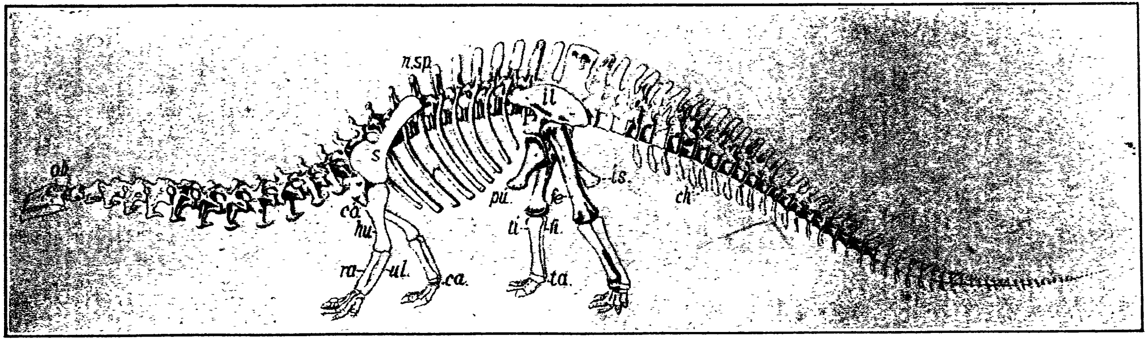


FIG. 188. — A dinosaur, *Brontosaurus*, from the Jurassic of the Rocky Mountain region. This reptile had a length of almost sixty feet; the head is remarkably small. *ca.*, carpal (wrist) bones; *ch.*, chevron bones; *co.*, coracoid; *fe.*, femur; *fi.*, fibula; *hu.*, humerus; *il.*, ilium; *is.*, ischium; *pu.*, pubis; *n.sp.*, neural spines; *ob.*, orbit of eye; *r*, ribs; *ra.*, radius; *s*, scapula; *ta.*, tarsal bones; *ti.*, tibia; *ul.*, ulna. (From Matthew.)

enable them, when feeding, to reach the surface to breathe. Some of the Jurassic and Lower Cretaceous forms were, so far as known, the largest land animals that ever lived on earth. *Brontosaurus excelsus* (Fig. 188), from the Morrison formation (Upper Jurassic and Lower Cretaceous) of the Rocky Mountain region, was about 60 feet long. From the same region and formation, Diplodocus was 80 feet long, and Atlantosaurus about the same length. Gigantosaurus from East Africa may have attained a still larger size.

The problem of *food supply* for such huge animals must at times have been very real. A full-grown Indian elephant weighing 8000 pounds eats 800 pounds of green fodder and 18 pounds of grain per day. A Brontosaurus with a probable weight of twenty tons would consume at least 4000 pounds of leaves and twigs. If these animals, like the living reptiles, were cold-blooded, they would eat somewhat less, but they may possibly have been warm-blooded. The difference between the daily rations of the warm-blooded lion and the cold-blooded crocodile of equal weights is very slight. A twelve-foot crocodile of 415 pounds weight eats 30 pounds of meat per day, while a full grown male lion weighing 500 pounds consumes in the active wild state 40 pounds of meat per day. (Data kindly given by Dr. Hornaday of the New York Zoölogical Park.)

3. Orthopoda (Predentata). Triassic to Upper Cretaceous. Some were bipedal, without armor (the Ornithopoda); others, with bony dermal plates, were at first bipedal, becoming later quadrupedal, with the heavier armor. The former group includes Iguanodon from Europe; Trachodon (with the front of the jaw expanded and resembling a duck's bill, 25 to 30 feet long), known from the Rocky Mountain region, New Jersey, North Carolina, and Georgia; and also some probably arboreal forms, like Thescelosaurus of the late Cretaceous of the Rocky Mountains and Great Plains. The armored group includes, among others, the Stegosauria and Ceratopsia (example, Triceratops). *Stegosaurus ungulatus* (Figs. 189, 190), from the Morrison formation (Upper Jurassic and Lower Cretaceous) of the Rocky Moun-

tains and the Upper Jurassic of Europe, was about 30 feet long and weighed at least 10 tons. It had probably the smallest brain (about 10 pounds) in proportion to its size of any land vertebrate, but to control the huge tail and hind limbs there was a very large expansion of the spinal cord in the region of the hip bones, making a sort of second brain, twenty times larger than that in the head. The animal was protected by numerous small,



FIG. 189. — A restoration of the reptile, *Stegosaurus ungulatus* (Fig. 190), by C. R. Knight. (From Lucas, through the courtesy of McClure, Phillips & Co.)

bony plates embedded in the skin of the head and neck, possibly also of the throat, and by two rows of huge, massive, triangular bony plates extending along the middle of the back from the head over two-thirds of the tail, the remaining one-third bearing four pairs of large spines. These plates and spines were in life covered by horny sheaths as is shown by their superficial vascular grooves. As the bones are solid the animals doubtless moved very slowly; this, added to their small head, small blunt teeth, and huge size necessitated an abundance of succulent

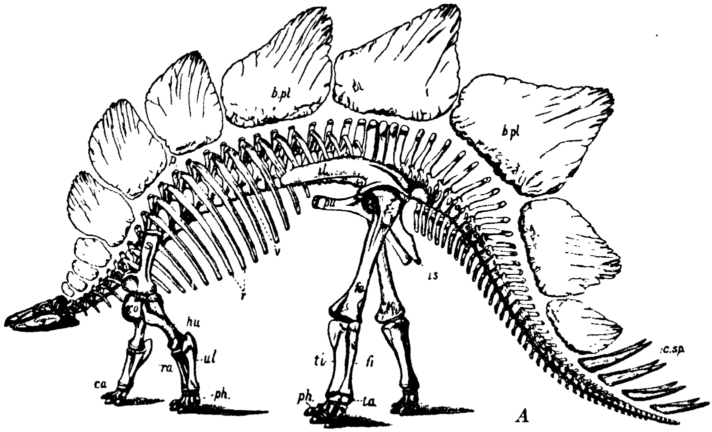
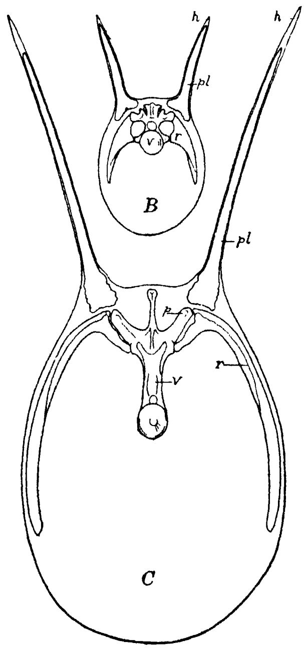


FIG. 190. — A thirty-foot-long dinosaur, *Stegosaurus ungulatus* Marsh, abundant during the Jurassic period upon the lands now occupied by the Rocky Mountains long before their upheaval into the present mountain system. *A*, entire skeleton. There should be double the number of large bony plates represented here, arranged in alternating rows, as in Fig. 189. Note the broad attachment of the rib to the back bone for the support of the heavy bony plates. *B*, ideal section through the neck, and *C*, through the trunk of the animal. *b.pl.*, bony plates, in life covered with horn; *ca.*, carpal bones; *co.*, coracoid, *c.sp.*, caudal spines; *fe.*, femur; *fi.*, fibula; *h*, encasing-horn; *il.*, ilium; *is.*, ischium; *p*, transverse processes; *ph.*, phalanges; *pl.*, bony plate; *pu.*, pubis; *r*, rib; *ra.*, radius; *s*, scapula; *ta.*, tarsal bones; *ti.*, tibia; *ul.*, ulna; *v*, vertebra. (*A*, from Marsh; *B*, *C*, from Lull.)



herbage near at hand; otherwise they would have died of starvation.

Immediately preceding the extinction of an order or family there is often a development of bizarre forms, as spinous shells and twisted cephalopods, representing apparently the remnant of developmental force in that family or order thrown out spasmodically just before its extinction. Stegosaurus is an

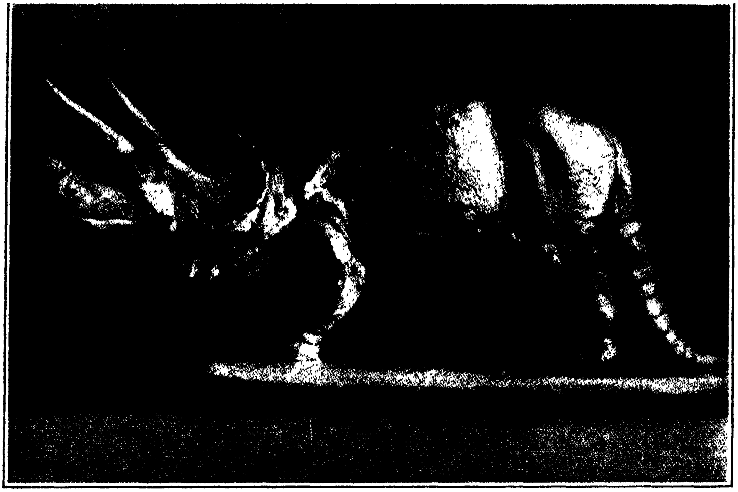


FIG. 191. — A restoration of the three-horned, *neck-frilled dinosaur*, *Triceratops prorsus*, living during the uppermost Cretaceous in the lowlands of what at present forms the Rocky Mountain area of North America. This reptile was twenty-five feet long. Restoration by Charles R. Knight. (From Lucas, through the courtesy of McClure, Phillips & Co.)

example of this among the dinosaurs; another excellent example is the Upper Cretaceous *Triceratops prorsus* (Fig. 191). This quadrupedal, herbivorous reptile with solid bones had a sharp cutting beak, a horn upon its nose, and a very large pair of horns on the top of its head, while the posterior part of the skull developed into a huge horn-covered frill margined with spines. This frill protected the top of the neck and gave to the skull its wedge-shaped appearance, the beak being pointed, bird-like.

Order 12. Pterosauria (Flying Reptiles)

Extinct flying reptiles with a long neck and a general bird-like build. The anterior of the two pairs of limbs are large, bat-like, leathery wings, the smooth membrane of which was supported between the greatly elongated little finger and the sides of the body (whence the name from Greek *pteron*, a wing, + *sauros*, a lizard). The thumb is vestigial; the other three fingers bear claws. Bones hollow and light. Breastbone with a keel. The power of flight was probably bat-like, more feeble than that of birds (Fig. 183).

The Pterosauria begin suddenly, fully differentiated, in the Jurassic and become extinct in the Upper Cretaceous. They vary in size from that of a sparrow to double that of an albatross. The earlier forms had sharp teeth. *Rhamphorhynchus* (Jurassic) had a long tail with an expanded membrane at its tip indicating very rapid turnings in its flight, which, with its long, sharp, slender teeth suggests that it was probably an insect feeder. *Pterodactylus* (Jurassic) had a very short tail. Some of the later forms were toothless, possibly fish-eating. Some huge ones (*Pteranodon*) from the Kansas Cretaceous had a skull over thirty inches long with a probable stretch of wings of twenty feet. The largest known living sea-bird, the albatross, has a stretch of wings of only twelve feet, with a weight of eighteen pounds.

1. Briefly define Reptilia. What is the significance of the name?
2. Name some ways in which the Reptilia represent an advance upon the Amphibia.
3. What is their geologic range?
4. What were their past habitats? Their present habitats?
5. Name the living orders into which the class Reptilia is divided; the extinct orders; give under each (*a*) their habitat, (*b*) a living and a fossil example where possible.
6. Why cannot the eggs of reptiles and birds be laid in water as are those of amphibians?
7. How do we account for the survival of the very primitive Hatteria?
8. What is the significance of the name Theromorpha?

9. How do you distinguish the Sauropterygia and the Ichthyosauria? What indication of a gizzard-like compartment in the stomach of the former?

10. What indications of evolution do you note among these?

11. Briefly define the order Dinosauria. What do we know concerning their external ornamentation? How?

12. Give the geologic range of the Dinosauria.

13. Amongst fossil vertebrates what is the chief means of telling a carnivorous form from a vegetable feeder? Which is the earlier type?

14. Describe an example of a carnivorous dinosaur; three examples of vegetable-feeding dinosaurs.

15. How did the probable amount of food eaten by a Brontosaurus compare with that required by an elephant?

16. Given only the footprints of an animal, what would be your procedure in making a restoration of the animal which produced it?

17. How may such bizarre forms as Stegosaurus and Triceratops be accounted for?

18. Give the distinguishing characters of Pterosauria, and the significance of the name; their size and geologic range.

19. How do Pterosauria resemble birds? How differ?

20. Define Crocodilia; Chelonia. Give a living example of each.

21. Distinguish the three divisions of the Squamata with an example of each.

CLASS H. AVES (BIRDS)

Body a compact mass with five spindle-like extremities. Thorax shifted very far back, hence the long flexible neck, and hence, too, the small head. Bones hollow and light.

The external *protective skeleton* consists of feathers, covering most of the body, a horny beak, claws on feet and sometimes on hands, and reptilian-like scales upon the lower portions of the legs and feet. The feathers are developed from reptilian-like scales fringing at their edges. The fore limbs are modified to form *wings*, upon the tips of which are three reduced fingers, representing probably the first, second, and third of the typical hand. There are four toes upon the hind limbs, the fifth toe of the typical foot being absent. In modern birds, one of the two rows of the ankle bones (tarsus) is fused with those of the foot, the other with the bones of the lower leg (tibia and fibula);

the joint is thus between the two rows of tarsal bones and not as in mammals between the bones of the lower leg and tarsus (Fig. 193). In all flying birds the breastbone has a well-developed keel for the attachment of the flying muscles.

Teeth are absent in all adult birds from the Tertiary to the present; Mesozoic birds had functional teeth. The œsophagus is dilated to form a crop for the storage of the food which is usually eaten so rapidly. From here the food passes to the stomach, a division of which, the *gizzard*, has in grain-eating birds (*e.g.*, pigeon) its wall so thickened with muscles and its inner lining so hardened and horny that, with the aid of the small stones the bird swallows, it forms an excellent grinding apparatus. In flesh-eating birds (*e.g.*, gulls, owls) it is thin-walled with a non-horny lining. If the gull is fed upon grain, its gizzard will gradually become thick, with a horny lining; the opposite effect will occur if the diet of the pigeon is changed to meat.

The excellent *respiratory* apparatus produces a higher body temperature (100° F.) than in any other animal; the air is pumped into the lungs and forced out by the elevation and depression of the breastbone, or back, or both. The lungs extend as prolongations all over the body and into many of the hollow bones. Birds thus agree with insects, the only other typically aërial class in having the fresh air carried throughout a large portion of the body and not only into the chest. The brain is large. The heart is completely four-chambered. The sense of smell is poorly developed, but those of sight and hearing are usually remarkably acute. Birds are *oviparous*. As the ovum or yolk passes down the oviduct it receives first the coat of white, or albumen, next a parchment-like membrane, and finally a calcareous coating, the shell, over all.

Migration is probably a habit derived from an instinctive search for favorable conditions for the rearing of young. Such conditions include a plentiful food supply and comparative freedom from enemies. Since the northern lands are snow-covered in winter and intensely cold, the abundance of life is

greatly limited as compared with the tropics. It thus follows that the birds that return north in summer find fewer enemies than in the south, while the seed-bearing plants and the insects are very abundant. Thus while the south provides an escape from winter, the north is ideal for the rearing of families.

Derivation of name. — Latin plural of *avis*, a bird.

Birds are exceedingly rare as fossils; their remains falling upon the surface of the land or water are quickly destroyed. The earliest known bird, *Archeopteryx*, is known only from two entire specimens and a single feather from the lithographic stone quarries (Upper Jurassic) of Solenhofen, Bavaria (Fig. 192). These indicate a reptile-like animal covered with feathers, and about the size of a small crow. It had sharp teeth, a short neck, claws upon each of the three fingers terminating the wings as well as the four toes of each foot, a small keel to the breast-bone (hence it could fly), shoulder girdle exceedingly small (for a flying bird), and a long tail composed of about twenty separate vertebræ with a pair of feathers attached apparently to each vertebra. During the remainder of the Mesozoic birds became more modern in appearance through the shortening of the tail by means of the consolidation of some of its vertebræ, the nearly universal loss of the claws from wings, and the lengthening of the neck.

Teeth did not disappear from the adult bird until the Tertiary. Avian remains from the Cretaceous include *Hesperornis regalis*, the diving bird three feet high, and the small flying Ichthyornis, both from Kansas (Figs. 183, 193). The Lower Eocene Diatryma is an example of the large flightless ground birds. Remains of these contemporaries of the little four-toed horse Eohippus have been found in Wyoming, New Mexico, and probably New Jersey. *D. steini* from Wyoming was seven feet high, with a skull 17 inches long, a compressed beak 6.5 inches high and 9 inches long, and a correspondingly massive lower jaw. One of the largest birds known is the but recently extinct *Dinornis maximus* from New Zealand, which stood twelve feet high.

In the late embryo of most modern birds, the tail consists of

five to ten separate vertebræ which later coalesce. Teeth are present in the embryo of certain species of parrot. A similar repetition of ancestral characters is seen in the *Hoactzin*, a native of the Amazon Valley. Directly after birth it makes climbing expeditions by means of its beak, feet, and the claws

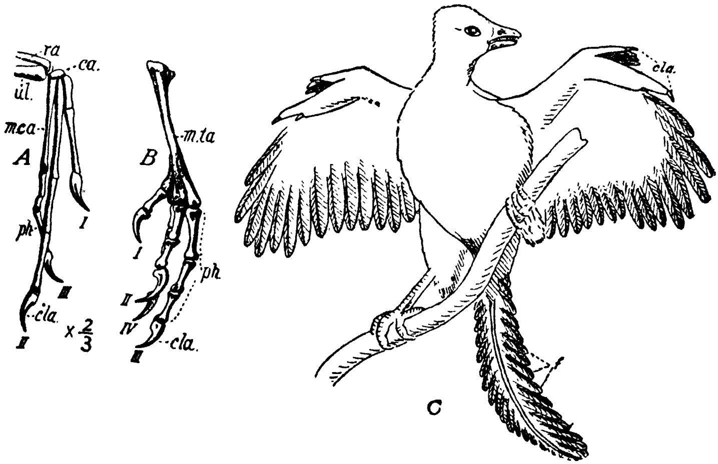


FIG. 192. — The earliest known bird, — *Archeopteryx*, of the size of a small crow, from the Upper Jurassic of Solenhofen, Bavaria. The jaws bear many sharp, conical teeth (there are 26 in the upper jaw). *A*, right hand (or wing bones). *B*, right foot. *C*, restoration. *ca.*, carpus (not well known); *cla.*, claws; *f*, distinct feathers, — each pair of these tail feathers is attached to a separate vertebra; *m.ca.*, metacarpal (palm) bones; *m.ta.*, tarso-metatarsals; the fusion of the metatarsals is not as complete as in modern birds; *ph.*, phalanges; *ra.*, radius; *ul.*, ulna; *I*, *II*, *III*, *IV*, digits, 1st (corresponding to thumb and great toe), 2d, etc. (*A* from Osborn, after Dames; *B* from Osborn, after Owen; *C* modified from Woodward's "Vertebrate Paleontology," after Pycraft.)

upon its wings. These claws disappear in the adult bird. In the young Hoactzin, as in Archeopteryx, the hand is longer than the forearm, but before the resorption of the claws the hand ceases to grow while the forearm becomes much longer, so that their relative lengths become reversed.

The penguins characteristic to-day of the southern part of the Southern Hemisphere had attained their specialization by the

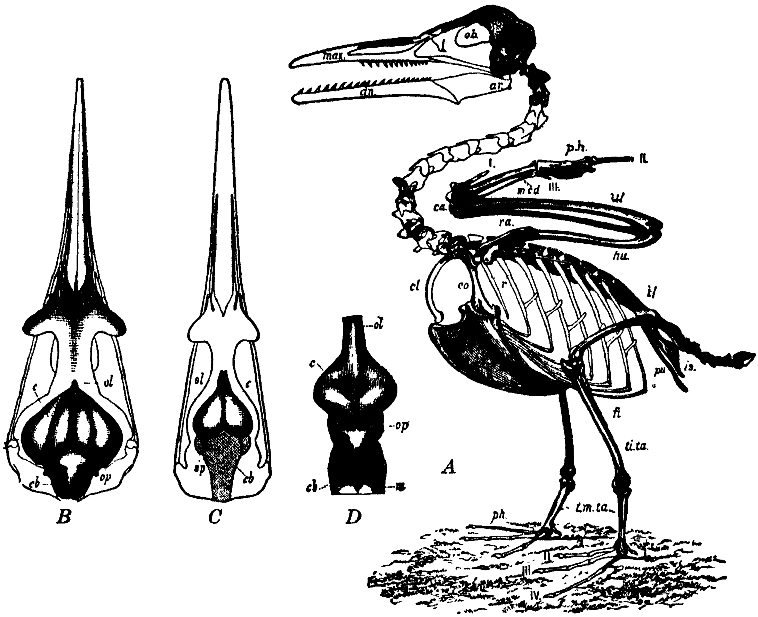


FIG. 193. — *Ichthyornis victor* Marsh, from the marine Niobrara beds (Upper Cretaceous) of western Kansas. It was slightly larger than a common pigeon. The hollow bones, strongly keeled breastbone and large wings indicate this to have been an excellent flyer, while its association with such universally marine forms as ammonites shows that it must have lived at least upon the borders of the sea. Though similar in general appearance to living birds, yet it shows its ancestry in its small, elongate, reptile-like brain (compare figures *B*, *C*, *D*, all drawn to same scale) and in its sharp, pointed, recurved teeth which are lodged in distinct sockets. *A*, restoration of entire skeleton. *B*, outline of the skull and brain cavity of the modern *tern*, seen from above. *C*, same view of *Ichthyornis victor*. *D*, cast of brain cavity of a *young alligator*. *ar.*, articular bone or mandible; *c*, cerebrum; *cb.*, cerebellum; *ca.*, carpal (wrist) bones; *cl.*, clavicle (the "wish bone"); *co.*, coracoid; *dn.*, dentary bone of mandible; *fi.*, fibula, — very small as in all modern birds; *hu.*, humerus; *il.*, ilium, — the hip bone; *is.*, ischium; *m*, medulla; *max.*, maxilla; *m.ca.*, metacarpals; *ob.*, orbit of eye; *ol.*, olfactory lobes of brain; *op.*, optic lobes of brain; *ph.*, phalanges (digit II has two phalanges); *pu.*, pubis; *r*, rib; *ra.*, radius; *ti.ta.*, tibio-tarsals, — the union of the tibia and proximal row of tarsals as is seen in the development of modern birds; *t.m.ta.*, tarso-metatarsal bones, — union of the distal row of tarsals with the metatarsals as is shown in the young of modern birds; *ul.*, ulna; *I*, *II*, etc., digits, 1st (corresponding to the thumb and great toe), 2d, etc. (After Marsh.)

Eocene; they occur in beds of that age in New Zealand and Antarctica. Likewise in the Eocene appeared ducks, herons, gallinaceous birds (such as primitive pheasants), vultures, owls, woodpeckers, and primitive Passeres. Fossils of most of these groups have been found in North America. This occurrence in the Eocene of families, and even at times of genera, which are living to-day is of especial interest in contrast with the mammals, of which not a single Eocene family is living to-day. In other words, the radiation of birds into the principal modern families took place before the Eocene, that of the mammals after that period. There is a great gap between the birds of the Eocene and the toothed birds of the Upper Cretaceous.

1. Give distinguishing characters of class Aves.
2. Distinguish the ankle-joint of reptiles and birds from that of mammals.
3. What is the significance of a keel to the breastbone?
4. Why do grain-eating birds swallow small stones? What difference between the gizzard of these birds and that of flesh-eaters?
5. What is the principal difference between the breathing apparatus of birds and that of mammals?
6. What is the possible origin of migration among northern birds?
7. Give the geologic range of birds.
8. Why are birds rare as fossils?
9. Describe Archeopteryx, distinguishing the reptilian from the avian characters.
10. Under what conditions were the lithographic slates of Solenhofen deposited?
11. What is the probable origin of birds?
12. In what ways do modern birds and especially the Hoactzin indicate their ancestry in their ontogeny?

CLASS I. MAMMALIA (MAMMALS)

Air-breathing, warm-blooded vertebrates usually with a protective exoskeleton of hair. The temperature of most mammals is about 98° F. The skull is articulated with the backbone by two rounded prominences (condyles), instead of by one as in birds and in most reptiles, and the lower jaw is articulated with

the skull directly without the aid of the separate quadrate bone present in those two classes. The teeth, typically forty-four in the placental mammals, are nearly always differentiated into three incisors on each side above and below, one fang (canine) and seven premolar and molar teeth. Molars are distinguished by having no milk teeth preceding them.

The ankle-joint is always between the bones of the lower leg (tibia and fibula) and the ankle bones (tarsus), never between the two rows of tarsal bones as in birds and reptiles. A muscular partition, the diaphragm (Fig. 173, *di.*), divides the body cavity into an anterior portion, the thorax, containing the completely four-chambered heart and the lungs, and a posterior portion, the abdomen, containing the digestive canal and the excretory and reproductive organs. All mammals, except the most primitive, the Monotremata, are viviparous; that is, the egg develops into a form more or less like the adult before leaving the body of the mother. The young, before birth, is nourished by the blood of the mother (except in the Marsupialia) through the placenta, a spongy membranous mass attached to the walls of the uterus; after birth by milk — the secretion of the mammary glands.

Most mammals, as the horse and deer, live upon the surface of the ground; some, as the squirrel and monkey, are arboreal or tree dwellers; rarely do they fly, as the bat; a few, such as the mole, are fossorial (burrowing); some, as the muskrat and beaver, have taken to an aquatic life in fresh waters, others, such as the seal and whale, to a marine life.

For discussion of a typical mammal see the cat, p. 383.

Derivation of name. — > Latin *mamma*, the breast. The young are nourished for a time after birth by milk secreted by the glands of the mother's breast.

Causes of extinction of mammals. — Animals with relatively larger brains being more alert, and adaptable to new conditions (Fig. 194), will survive in competition with smaller-brained forms; they will also get more food and take better care of the young. Other characters, besides defective brain,

which gradually lead to the extinction of their possessors are inadaptive tooth and foot structure, excessive bulk, or extreme specialization in some direction, such as an exceptional development of organs of combat (*e.g.*, horns). Growing aridity, with the consequent drying up of water courses, is another powerful factor in extinction. For example, the growing aridity of the Pliocene in the Rocky Mountain region and the Great Plains region to the east, seen also in the sandy nature of the stratigraphic deposits as well as in the peculiar fauna and flora, was most probably the cause of the extinction of the rhinoceroses as well as of some of the browsing types of horses and camels.

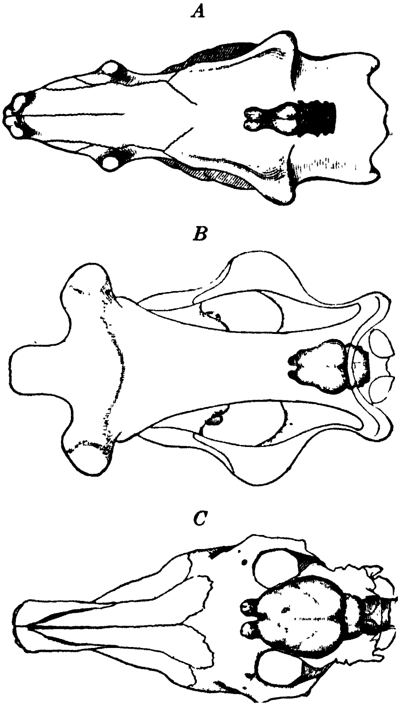


FIG. 194. — A comparison of relative size of brains of ungulate mammals from the Eocene to the present. *A*, outline of skull of the Eocene *Uintatherium mirabile* Marsh with cast of brain in position. (× $\frac{1}{16}$.) *B*, same of *Brontotherium ingens* Marsh (× $\frac{1}{20}$) from the *Miocene*. *C*, same of the *modern horse*, *Equus caballus* Linn. (× $\frac{1}{12}$.) (From Marsh.)

During early and mid-Pleistocene time North America was covered with herds of mastodons, many varieties of elephants, large llamas, camels, and enormous numbers of horses; of the last there were at least ten species. Prong-horn antelopes, white-tailed deer, peccaries, giant sloths, and glyptodonts were also abundant. (The moose, bison, mountain goat, musk-ox, red deer, bear, and reindeer did not arrive from Eurasia until near the

close of the Pleistocene.) Preying upon these were the saber-tooth tigers as well as large, lion-like cats and giant dogs. The extinction of the majority of these Pleistocene mammals was probably mostly due, either directly or indirectly, to the accompanying glacial conditions. Exceptionally cold waves or unusually prolonged cold seasons even now lead to a temporary diminution in the number of animals in a herd. This may be due to the freezing of the young and other weak members, complete starvation from the deep covering of snow over their food, or merely partial starvation and a consequent inability of the individual females to protect their young from the Carnivora. This reduction of the herd may in turn lead to its complete destruction through the insufficiency in the number of bulls to protect the young; the reduction in the number of herds leads in turn to inbreeding and to its probable accompaniment of infertility. Infertility may likewise often be produced by an increasingly unfavorable climatic environment. The change from a forested condition, such as existed in the Northern Hemisphere north to the Arctic Ocean during the early Pleistocene, to an unforested one, and back again during times of increasing moisture, as happened at least once during the Pleistocene, would cause the diminution of both forest animals, such as the browsing camels, browsing horses, mastodons, elephants, tapirs, and deer, and of grazing animals. The remains of the larger Pleistocene animals, now extinct, are nearly always associated with evidences of forests. It has been suggested that a corollary cause in the extinction of the horse from North America may have been some epidemic disease, or diseases, carried by some fly, tick, or other parasite-bearing insect; the multiplication and spread of such insects are increased by the presence of a moist climate. If southern North America, accordingly, was exceptionally moist during the various southward advances of the Pleistocene ice sheets, of which there is evidence, some such insect-spread epidemic may have led to the extinction of the horse and other grazing animals by the close of the Pleistocene.

Mammals may be divided into the following orders:

The orders of mammals represent an ascending series as follows: (1) The very primitive, reptile-like subclass *Prototheria* (represented by Order 1). These are egg-layers; the egg is (in *Echidna*) placed by the mother in a ventral pouch containing milk glands without nipples; here it is hatched and then nourished by the milk poured out around it. *Ornithorhynchus* lays its eggs in a nest in its burrow, brooding over them bird-like. The body temperature is variable (changing as much as 15° according to the temperature of the environment). A cloaca is present, in which terminate the ducts of the urinary, reproductive, and digestive systems. They have many reptilian characters in skull and skeleton. (2) The more advanced subclass *Metatheria* (including Order 2). They produce the young alive, but in so rudimentary a condition that directly after birth they are placed by the mother in a ventral pouch which contains the false nipples and are there sheltered until able to take care of themselves; a placenta is absent or functional only for a short period. Cloaca absent. (3) The subclass *Eutheria* (including Orders 3–11) are the most highly evolved. The young are nourished through a placenta until well advanced (whence the name *placental mammals* for this subclass); after birth they are nourished by milk through true nipples. The young are never carried in a pouch. Cloaca absent.

Order 1. Monotremata (Egg-laying Mammals)

Principal characters given above under subclass Prototheria. Name from Greek *monos*, one, + *trema*, opening, in allusion to the cloaca.

No remains of this order have with certainty been found before the Pleistocene. The two living genera, duck bill (Ornithorhynchus) and the spiny anteater (Echidna), are confined to the Australian region.

Order 2. Marsupialia (Marsupials)

Chief characters given above under subclass (2), the Metatheria. Name from Latin *marsupium*, a pouch, in allusion to the ventral pouch for carrying the young. This large order includes carnivorous and insectivorous types as well as hoofed and rodent-like forms.

If we place within this order the possibly marsupial carnivorous suborder Triconodonta (Jurassic; including Triconodon and Phascolotherium) and the herbivorous, North American, European, and South African suborder Multituberculata (Upper Triassic to Paleocene, including the Jurassic Plagiaulax and the Paleocene Polymastodon from the Puerco of New Mexico), this order is known from the Upper Triassic to the present. The opossums, now confined to North and South America, are known here since the Cretaceous and in Europe during the Lower Tertiary. Originating in America and found here as fossils since the Upper Cretaceous, opossums possess one of the longest genealogies of any living animal. Except for the American opossums and Cænolestes, all marsupials are at present confined to the Australian region; they include the Tasmanian wolf and bandicoots of the *polyprotodonts*, or marsupials with many front teeth of equal size, and the kangaroos, wombats, and flying phalangers of the herbivorous *diprotodonts*, or marsupials with two enlarged incisors. Representatives of both of these groups were living in South America during the Tertiary.

Order 3. Insectivora

Small mammals, eating worms and insects (whence the name).

These have a low type of brain and occur from the Jurassic to the present. Representatives of the extinct family Pantotheria (Trituberculata) have been found in the Jurassic and Cretaceous of North America, Europe, and Mongolia. They unite the characters of the earliest carnivores and insectivores. The living families of the moles, shrews, and hedgehogs have existed since the Oligocene.

Order 4. Chiroptera (Bats)

Mammals with the fore limbs modified to form wings by the development of a broad web between the greatly elongated fingers (usually the second to fifth) and the sides of the body and the hind limbs (hence the name from Greek *cheir*, a hand, + *pteron*, a wing). Breastbone with a keel for attachment of flying muscles.

This order is known from the basal Eocene of Colorado to the present, and now includes the fruit-eating bats of the tropics of the Eastern Hemisphere and the insect-eating bats so abundant throughout the world.

Order 5. Carnivora (Flesh-eating Mammals)

Fur-covered, flesh-eating mammals (whence the name from Latin *carnis*, flesh, + *vorare*, to devour); all teeth have cutting edges.

This order is known from the Eocene to the present. It includes: (1) the extinct primitive *Creodonta* (Basal Eocene to Lower Oligocene, mostly of North America, but also of Europe and Africa). These are such generalized types that they are only with difficulty distinguished from the Eocene Insectivora and Ungulata. As they do not possess well-developed carnassial teeth (see below under Fissipedia), they are not perfected as flesh-eaters. Examples of these are Mesonyx and Patriofelis (Fig.

195, 2–4), both from the Middle Eocene (Bridger) of the Rocky Mountains, and Hyænodon from the Oligocene. (2) *Fissipedia*, or Carnivora Vera (Upper Eocene to present); last premolar above and first molar below, called carnassials, always specially modified for cutting and bruising; in front of these the teeth are always compressed and pointed; behind them they have broad, tuberculate surfaces. The dog tribe (Canidæ, comprising dogs, wolves, jackals, and foxes) made its appearance in the Eocene, passing through the greater part of its development in North America. The cat tribe (Felidæ) is first known from the Oligocene; both living and as fossils they are found throughout the world, except the Australian Region. Here belong the huge saber-tooth tigers, Machairodus (Pliocene and Pleistocene of Europe), and Smilodon (Fig. 196, 7), Pleistocene of North and South America. The raccoons (Miocene to present) are an American family. The bear tribe (Ursidæ) came in with the Miocene; it originated in Eurasia and did not reach North America until the Pliocene; during the Pleistocene the great cave-bear (*Ursus spelæus*) of Europe was hunted for food by contemporaneous man. The different branches of the Fissipedia converge as they are traced back into the lower Tertiary, pointing to a common ancestor in the Eocene. (3) The *Pinnipedia* (Miocene to present) have limbs adapted to aquatic life. They may have descended from forms allied to the creodont Patriofelis. They are represented at present by the seals and walruses.

Order 6. Rodentia (Rodents or Gnawing Mammals)

Small, fur-covered, vegetable-feeding mammals without canine teeth and usually with only two long, chisel-like, continuously growing incisors in each jaw. The typical incisor, seen in most modern rodents, such as rats, mice, squirrels, and beavers, has the enamel confined to a band upon the anterior face; since the remainder of the tooth consists only of the softer dentine, a most efficient, continually sharpened chisel is the result (whence the name from Latin *rodens*, gnawing). Eocene to present.

Rodents today exceed all other mammalian orders in number

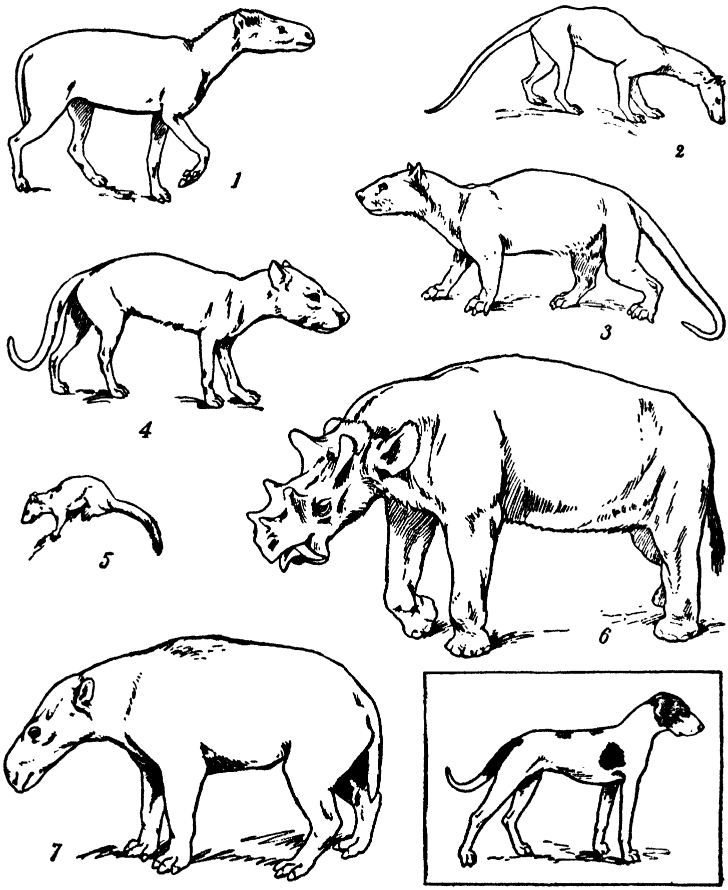


FIG. 195. — Outline restorations of some of the more characteristic mammals living in North America during Upper Eocene (Bridger) time. These are reduced to a uniform scale, with a pointer dog (in the frame) to show relative sizes. *1*, a primitive *rhinoceros* (*Hyrachyus eximius*). *2–4* are *creodonts*, — primitive Carnivora. *2*, *Tritemnodon agilis*, a form with hyena-like teeth. *3*, *Patriofelis ferox*. *4*, *Dromocyon velox*, a big-headed, wolf-like form, though with a very small brain cavity. *5*, a primitive *rodent* (*Paramys delicatior*). *6*, the huge *ungulate*, *Uintatherium alticeps*. This had an extremely small brain. *7*, one of the smaller early *titanotheres* (titanic beasts), *Mesatirhinus superior*. (From Scott.)

of genera and species. Rabbits, beavers, and porcupines are known since the Oligocene, rats and mice since the Pliocene (Figs. 195, 5 and 196, 5.)

Order 7. Edentata (Sloth, etc.)

Dentition imperfect (*i.e.*, incisors and canines usually absent, premolars and molars without roots or enamel) or teeth entirely absent (whence the name from Latin *e*, without, + *dens*, a tooth).

These degenerate mammals may possibly have evolved from the common ancestors of the rodents and ungulates through the extinct Tæniodonta (Ganodonta) from the Paleocene of North America. The earlier tæniodonts have well-developed, rooted, and more or less completely enameled teeth; in the later forms the teeth lose their roots and most of the enamel. True edentates are known from the Eocene to the present and from all continents except Australia. No fossil remains of the modern sloths (Bradypodidæ) and anteaters (Myrmecophagidæ) are known; these two families are combined in the extinct ground sloths (Megatheriidæ) which have the head and teeth of a sloth and the tail of an anteater (Fig. 196, 2); a late American genus (*Megatherium* of the Pleistocene) of this family is the largest-known edentate, one species attaining a length of almost twenty feet. Armadillos are found as early as the Eocene; one of the largest genera known is *Glyptodon* from the Pliocene of North and South America with a rigid, usually ornate carapace; this animal attained at times a total length of fifteen feet.

Order 8. Ungulata (Hoofed Mammals)

Land-dwelling mammals with the weight of the body usually resting upon the ends of the toes which are nearly always invested by solid horny nails, the hoofs. (Hence the name from Latin *ungula*, a hoof.) Canine teeth absent or small; premolars and molars large, their broad crowns beset with ridges or tubercles.

In the lowest Eocene it is almost impossible to distinguish the ancestors of mammals with claws (the *Unguiculata*, including orders 3–7) from those with hoofs (the *Ungulata*). They are

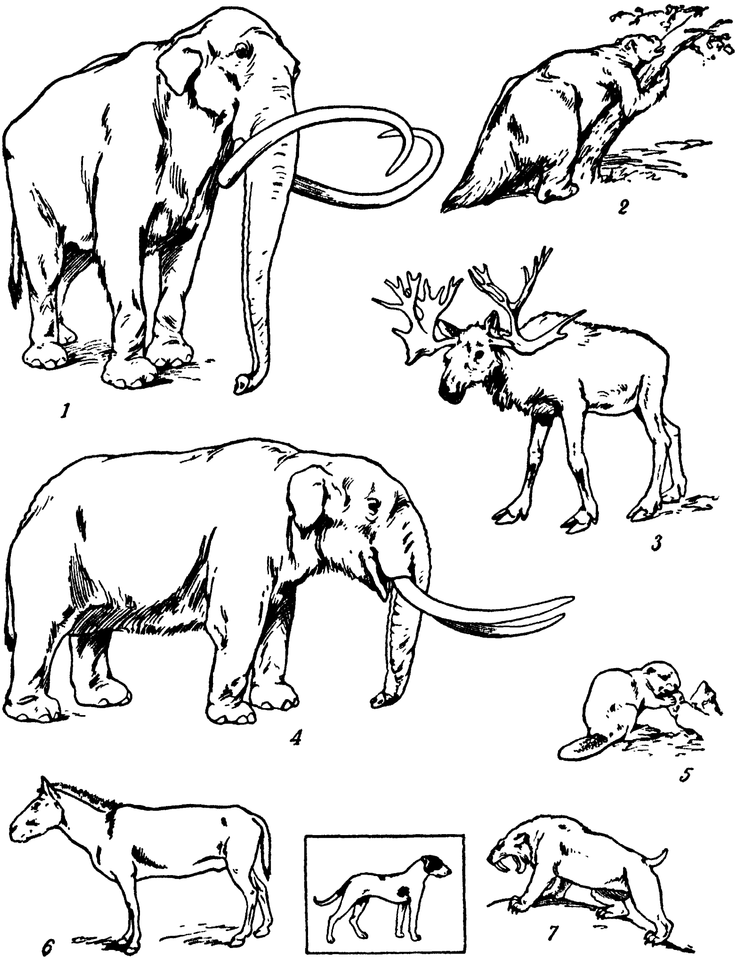


Fig. 196. — Outline restorations of some of the more characteristic mammals living in North America during the Ice age (Pleistocene). These are reduced to a uniform scale, with a pointer dog (in the frame) to show relative sizes. Note the difference in size between these and the Eocene mammals (Fig. 195). *1*, the Columbian elephant (*Elephas columbi*). *2*, the giant ground-sloth (*Megalonyx jeffersoni*), an edentate. *3*, stag-moose (*Cervalces scotti*), one of the artiodactyl ungulates. *4*, the American mastodon (*Mammut americanum*). *5*, the giant beaver (*Castoroides ohioensis*), a rodent. *6*, Texas horse (*Equus scotti*). *7*, saber-tooth tiger (*Smilodon californicus*). (From Scott.)

both flat-footed, five-toed animals with the toes terminating in nails intermediate between claws and hoofs, with freely movable fore limbs and tuberculate molar teeth, the tubercles in the former being slightly more pointed and cutting than in the latter. The primitive Ungulata were mostly small, inhabiting marshes or forests, with teeth adapted to succulent herbage. Many

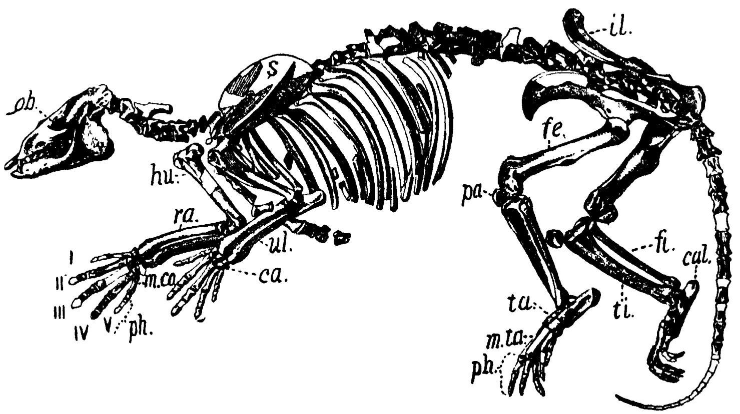


FIG. 197. — A primitive light-limbed, omnivorous, hoofed mammal. *Phenacodus primævus* Cope, one of the Condylarthra, from the Wasatch (Lower Eocene) of Wyoming. This animal, somewhat larger than a sheep, was in this case exceptionally well preserved. It is shown here, laterally crushed, just as it occurred in the rocks. *ca.*, carpal (wrist) bones; *cal.*, calcaneum; *fe.*, femur; *fi.*, fibula; *hu.*, humerus; *il.*, ilium; *m.ca.*, metacarpal (palm) bones; *m.ta.*, metatarsals; *ob.*, orbit of eye; *pa.*, patella; *ph.*, phalanges (toes); *ra.*, radius; *s*, scapula; *ta.*, tarsal bones; *ti.*, tibia; *ul.*, ulna; *I, II, III, IV, V*, digits, 1st (corresponding to thumb and great toe), 2d, etc. (After Cope.)

branches of these early Ungulata (which were probably not developed from any of the Condylarthra known at present) became modified during the course of the Tertiary into hard-hoofed dwellers of the dry, upland plains with teeth capable of grinding the dry grasses. Grasses were probably established as a rather dominant factor in the earth's vegetation by the time of the Upper Eocene, though the siliceous grasses, now constituting the grasses of the plains, probably did not come into

prominence until the Miocene. As the Tertiary is ascended, especially during the Oligocene, Miocene, and Pliocene, there is a reduction in the number of browsing and ambulatory animals and an increase in the grazing and cursorial types. The principal advance in the mammals lay, however, in the enlargement of the brain (Fig. 194).

The Ungulata include among others the following eight suborders:

1. The most primitive of the Ungulata are the extinct Condylarthra (Paleocene and Lower Eocene), difficult of separation

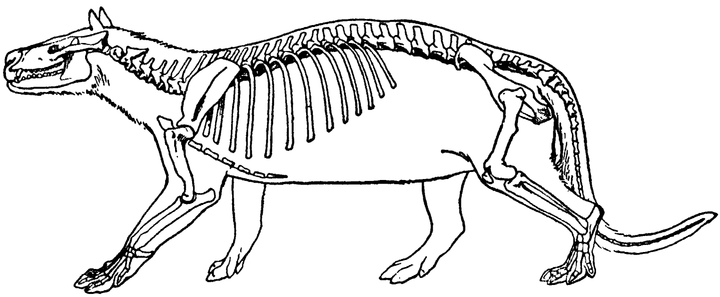


FIG. 198. — Restoration of skeleton of *Phenacodus primævus*, from the Lower Eocene (Wasatch). This is one of the Condylarthra, — an exceedingly primitive group of ungulates which serve to connect quite intimately the hoofed and clawed mammals. (From Scott.)

from the early Carnivora — the Creodonta. They are light-limbed animals with five digits, a small brain, and usually with forty-four short-crowned and tuberculate teeth. The best-known example is Phenacodus from the Lower Eocene (Figs. 197, 198).

2. Hyracoidea (Lower Oligocene to present). These small rock- and tree-living hoofed animals include the coney (Hyrax) of Africa and southwestern Asia.

3. Amblypoda (Paleocene and Eocene) confined mostly to North America. Huge, heavy-limbed, blunt-footed animals, they include the huge hippopotamus-like Coryphodon, also the giant Uintatherium (Dinoceras) (Fig. 195, 6) and Eobasileus,

with three pairs of bony, horn-like prominences upon the top of the skull.

4. The Proboscidea, the elephant tribe (Upper Eocene to present), are primitive ungulates. Each of the massive limbs terminates in five toes which are separately incased in hoofs (Fig. 199). Canine teeth are absent; the molars are large and transversely ridged. These molars (Fig. 200) come in successively from behind and move obliquely forward to be finally, when worn down very low, pushed out from the front of the jaw. Owing to the great size of the teeth and the shortness of the jaw, only one tooth on each side, above and below, is in full use at one time. In existing forms there is only one pair of incisors present, the upper; these are free from enamel and are developed into continuously growing tusks. Many early forms had tusk-like incisors both above and below (*e.g.*, Paleomastodon (Fig. 201) of the Upper Eocene of northern Africa). As is true of all animals, there is seen in the elephant a persistence of primitive, archaic



FIG. 199. — Vertical section through the fore foot of the Indian elephant. *U*, lower end of ulna; *L*, lunar bone of the carpus (wrist); *M*, magnum of carpus; *III*, third metacarpal (palm) bone; *1*, *2*, *3*, phalanges of the third digit (middle finger); *E*, pad of elastic tissue. (From Scott, after M. Weber.)

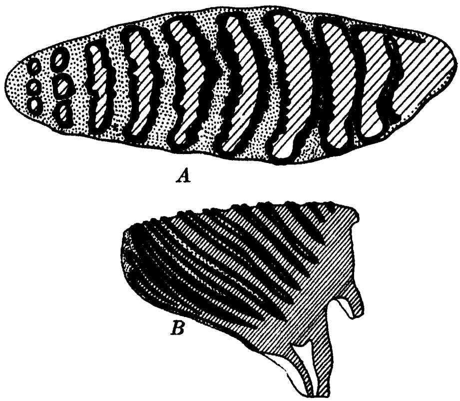


FIG. 200. — Molar tooth of an Indian elephant. *A*, crown view much reduced in size. *B*, longitudinal section. Black portion enamel; dotted, cement; cross-lined, dentine or ivory. Shows the deep infolding of the enamel and its projection as grinding ridges. (After Lull.)

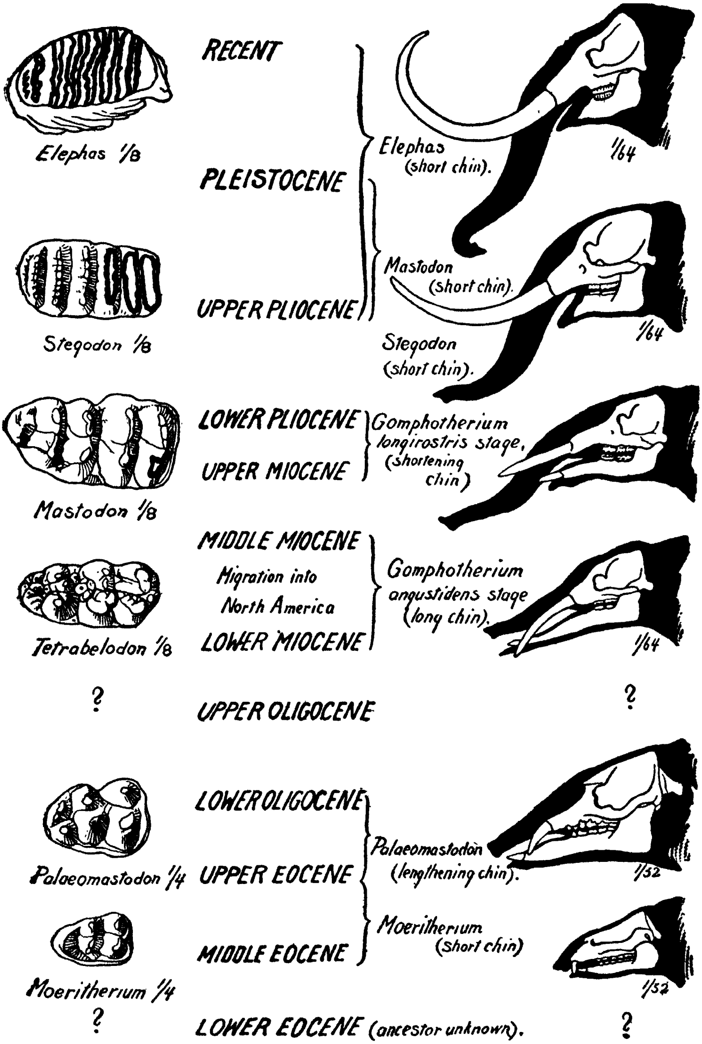


FIG. 201. — The evolution of the elephants: right, the skull, with the proboscis restored in black; left, the last lower molar. Principal changes are increased height of the skull and its decreased length with less teeth in consequence, also development of a long snout or trunk and increased length of two or four incisors into tusks. (Tetrabelodon should read Gomphotherium.) (From Scott, after Lull, modified by Sinclair.)

characters alongside of highly adaptive, modern ones. The elephant retains the primitive mammalian form of body, the five toes and the carpal bones arranged in vertical rows, but these are associated with such highly specialized characters as reduction in number of teeth, remarkable growth of two incisors, wonderful increase in height of skull due to the development of air cavities, and the acquirement of the muscular trunk.

According to present evidence the evolution of the elephant (Fig. 201) began in northern Africa with the mid-Eocene swamp-dweller, Mœritherium; this seems to have had a prehensile upper lip, since the nasal bones were beginning to recede. This recession of the nasal bones became more and more marked, indicating thus a longer and larger trunk, in the line ascending into the modern elephant (Elephas), *i.e.*, Paleomastodon, Gomphotherium, Mammut, Stegodon, Elephas. The first of these, like its ancestor, Mœritherium, was confined to northern Africa, the rest had migrated more or less fully over the entire Northern Hemisphere during the Miocene and reached South America in the Pleistocene.

In North America the most conspicuous and abundant species during the Pleistocene (Fig. 202) were — (*a*) the American mastodon (*Mammut americanum*) ranging from Alaska and California to Prince Edward Island, Florida, and Central America (Fig. 196, 4). The teeth were comparatively small so that two or three could be in use simultaneously upon each side in each jaw. (*b*) The mammoth (*Elephas primigenius*), with height usually less than 9 feet, and abundant throughout the Northern Hemisphere. It is of this species that complete carcasses have been found frozen in the sands and gravels of northern Siberia along the Lena River. That it was adapted to a life in a cold climate is shown both by its dense, woolly short hair covered with long outer hair, and by the contents of the stomach, remnants of present-day Siberian vegetation. (*c*) The Imperial elephant (*Elephas imperator*), attaining a height of over thirteen feet and ranging at least from Ohio to Mexico City. (Among the existing African elephants the male often attains a height of over eleven

feet.) The mastodon (Mammut) was more of a forest dweller than Elephas; its low-crowned teeth had each two to five high ridges for crushing the succulent herbage, especially the twigs of coniferous trees, while the true elephant (Elephas) with its high-

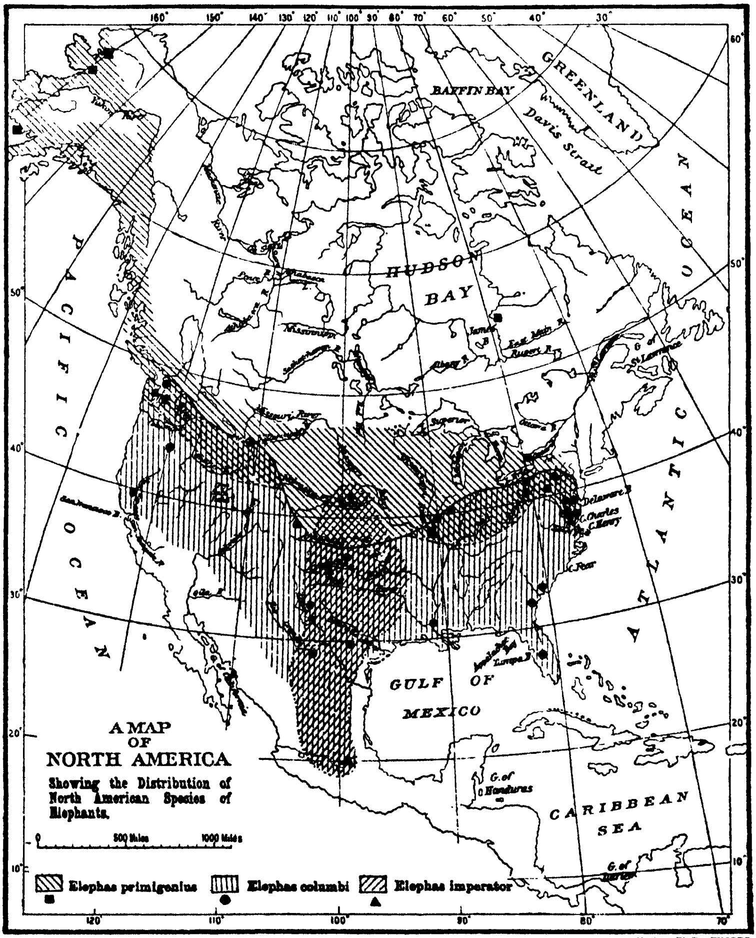


FIG. 202. — A map showing the widespread distribution of elephants in North America during the Pleistocene. (From Lucas.)

crowned teeth, each with ten to sixteen very low ridges, can grind the harder grasses of more open regions.

5. Embrithopoda (Upper Eocene and Oligocene of Africa). A well-known genus is *Arsinoitherium* — large, rhinoceros-like animals, some almost six feet high at the shoulders, with a pair of huge, pointed, forwardly directed horns over the snout and a smaller pair above the eyes.

6. Litopterna (Eocene to Pleistocene of South America). Some of these animals paralleled the horses in their development, but their more primitive character is shown in their smaller brain, less adaptive skeletons, and lower-crowned molars. The number of toes varies from five to one in different genera, but the third is always the longest. Examples are: Macrauchenia (Pleistocene), three toes on both fore and hind feet; Thoatherium (Miocene), a small animal with but one toe on fore and hind feet like the existing horse.

7. Perissodactyla, odd-toed ungulates (Lower Eocene to present). In these, the *odd-toed* ungulates, the third toe on both fore and hind foot is the longest (whence the name from Greek *perissos*, odd, + *dactylos*, a finger). The plane of symmetry of the foot bisects the third digit. Examples include: (*a*) tapirs and rhinoceroses, both of which families date from the Eocene, and were present during the Tertiary upon most of the continents. Both disappeared from North America after the Pliocene. The rhinoceroses very probably originated in North America (Fig. 195, 1). Baluchitherium, the largest known representative of the rhinoceros family, stood about thirteen feet high at the highest part of the back. (*b*) The huge titanotheres (Figs. 195, 7 and 203), some of the later members of which attained a height of eight feet and a length of fifteen feet, existed during the Eocene to Oligocene.

(*c*) The horse family (Equidæ) dates from the Lower Eocene in both North America and Eurasia. Fossil remains of the horses are most abundant and their genealogy very complete. The family branched from a so far undiscovered five-toed primitive ungulate, which gave rise in time to the four-toed Lower Eocene

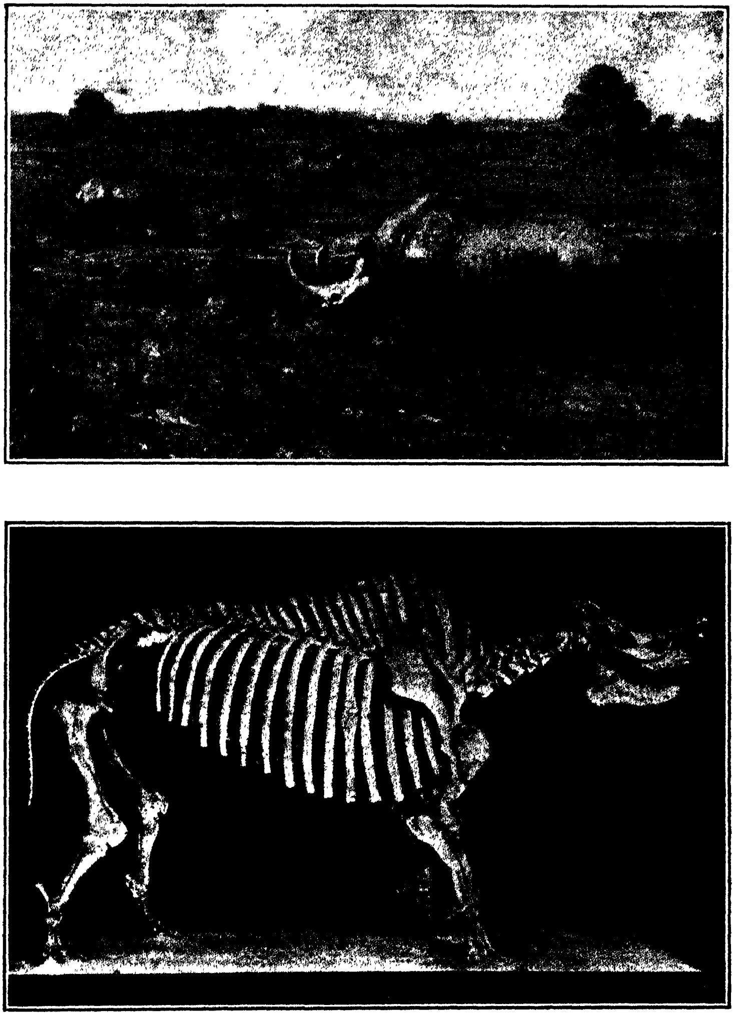


FIG. 203. — Above: Typical scene in western North America during the Lower Oligocene time, showing a small herd of *titanotheres* of the genus Brontotherium. The individual in the foreground is a male. Below: A skeleton of a female *Brontotherium gigas* from South Dakota. Note the small nasal horns in comparison with their tremendous development in the male above. (From Osborn.)

Eohippus of Europe (Fig. 204). This tiny animal, less than a foot high, migrated across Asia into western North America, where the evolution (Figs. 205–207) of the modern horse (Equus) was completed, giving an ascending series somewhat as follows: Eohippus (Lower Eocene), Protorohippus (Mid-Eocene), Oro-



Fig. 204. — A restoration of the earliest known ancestor of the modern horse, Eohippus, — the Dawn Horse, from the Lower Eocene (Wasatch) of western North America. In size these varied from that of a cat to a small fox. Note the short face (distance from eye forwards), short neck, arched back, short limbs and similarly short feet, with several divergent toes upon each. (From Scott.)

hippus (Upper Eocene), Epihippus (topmost Eocene), all more or less fully four-toed but increasing in size. The line is continued in Mesohippus (Lower Oligocene), the two-foot-high Miohippus (Upper Oligocene), both three-toed with the side toes touching the ground, through the three-foot-high Merychippus (Miocene), three-toed but side toes not touching the ground and hence

almost functionless, into the typical grazing horse — the one-toed Equus (Pliocene to present), with the side toes reduced to bony splints at the sides of the leg bone. The embryo of the modern horse passes through at least some of these stages in its development. For example, a horse embryo fourteen inches long has three toes with well-developed metacarpal and pha-

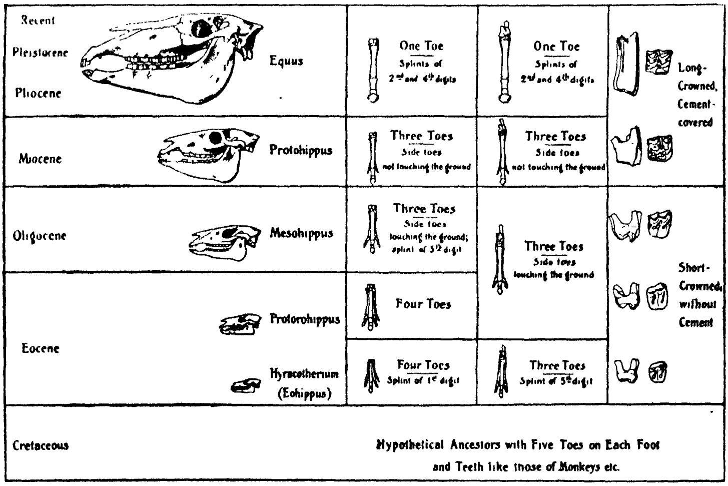


FIG. 205. — Evolution of the horse. I. (Drawn to same scale.) Note the increase in vertical diameter of the skull, the movement of eye backwards (hence increase in length of face), the increase in height of teeth accompanied by an infolding of cement between the enamel ridges of each tooth and the decrease in number of toes upon both fore and hind feet. Protohippus represents a stage of evolution somewhat similar to Merychippus. (After Matthew.)

langeal structures, resembling Miohippus. Merychippus shows well its intermediate position between the browsing and grazing type of horse in its teeth; its milk teeth are short-crowned and without a covering of cement like its ancestors; its permanent set are long-crowned with cement filling the spaces between the enamel ridges, as in its descendant Equus. This change from the little Eohippus, the "dawn horse," to the large modern horse took place through changes in all parts of the skeleton. Besides

increase in size of most bones in the body, the succeeding descendants walked more and more upon the ends of the toes. Since the series began by having the middle digit the longest, this digit gradually assumed the weight of the body. The arched back likewise became straight, and the molar teeth changed from a rooted, low-crowned, cement-free type adapted only to browsing, to one growing until an advanced age and hence high-crowned, usually without roots, and cement-covered. This type of tooth is well fitted for grazing, for the soft cement and hard enamel are folded down into the dentine, which is intermediate in hardness, and consequently the grinding surface is always rough from the projecting enamel ridges (compare with Fig. 200). During the Pliocene and Pleistocene (Fig. 196, 6) Equus migrated from America into all other continents except Australia, over the land connections then existing. It had, however, become extinct in North and South America before the time of Columbus; all wild horses here are escaped descendants of those brought in by European explorers.

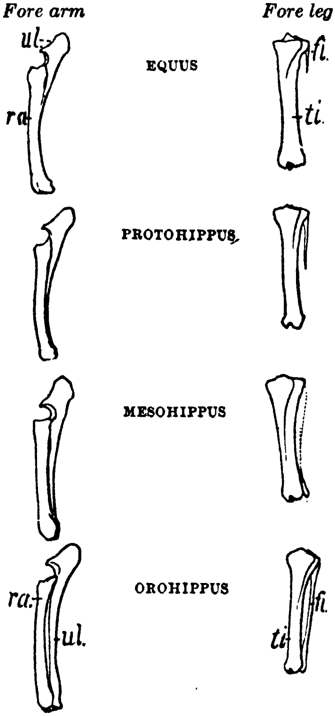


FIG. 206. — Evolution of the horse. II. (Not drawn to scale.) In the course of evolution from Orohippus (Upper Eocene) to Equus, the bones of the fore arm (radius and ulna) gradually became consolidated into one bone, resulting in the disappearance of the lower end of the ulna. In the fore leg (fibula and tibia) the fibula was gradually obliterated. These changes resulted in a more slender limb and hence greater speed. *fi.*, fibula; *ra.*, radius; *ti.*, tibia; *ul.*, ulna. (After Marsh.)

The evolution of the horse thus occurred upon the North American continent in the era immediately succeeding its elevation from the

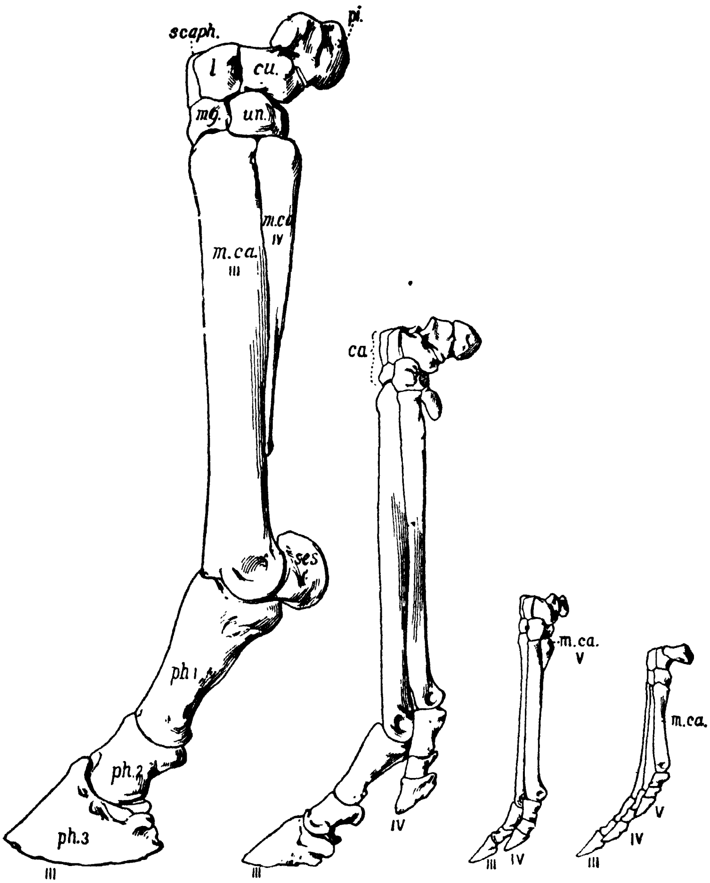


FIG. 207. — Evolution of the horse. III. The left fore foot (viewed from the left side) of the one-toed Upper Pliocene, Pleistocene and modern horse, Equus; the three-toed Miocene horse, Merychippus; the three-toed Oligocene horse, Mesohippus; and the four-toed Eocene horse, Eohippus. All are drawn to same scale. According to Scott (see Fig. 204) the toes should be almost horizontal. *ca.*, carpal (wrist) bones; *cu.*, cuneiform; *l*, lunar; *m.ca.*, *III*, *IV* and *V*, metacarpal three, four and five; *mg.*, magnum; *ph. 1*, *2* and *3*, proximal, middle and terminal (ungual) phalanges; *pi.*, pisiform, — the ulnar sesamoid bone developed in the tendon of the flexor muscle; *ses.*, the sesamoid bone developed in the tendon behind the junction of the metacarpus and phalanges; *un.*, unciform; *III*, *IV*, *V*, the digits. (After Matthew.)

Cretaceous seas. At the beginning of this Cenozoic Era the warped land surface was necessarily occupied by many swamps, lakes, and aggrading stream beds. Later, the filling up of these depressions, accompanied by the growing aridity produced by the increasing elevation of the land to mountain heights, led to the drying up of many water courses and to the necessity of greater speed in the inhabitants to reach food and water. The incoming of the more siliceous grasses about the middle of this era, which adapted themselves to this more arid climate, placed a premium also upon longer and better grinding teeth.

8. The Artiodactyla, even-toed Ungulates (Lower Eocene to present). In these, the *even-toed* ungulates, the third and fourth toes of both fore and hind feet are the longest and are of equal size (whence the name from Greek *artios*, even, + *dactylos*, a finger). The plane of symmetry of the foot passes between the third and fourth digits. In the earlier forms the grinding teeth are low-crowned and tuberculate; later (in cattle and antelopes) these tubercles unite to form continuous crescents, and the crown becomes almost as high as in the horses among the Perissodactyla. *Pigs* (*Suidae*), dating from the Middle Eocene, are the least modified descendants of the early Artiodactyla; even the canine teeth are pretty well retained. True pigs (Sus), known from the Upper Miocene to the present, had, up to the time of Columbus, always been confined to Eurasia and Africa. Another very primitive family, that of the Hippopotami, now confined to Africa but formerly found throughout Eurasia and Africa, has thus far been traced back only to the Lower Pliocene.

It is likely that all lower Tertiary Artiodactyla, like the primitive existing forms noted above, possessed a simple stomach and did not chew the cud; this power was probably accompanied by the development of the crescent-shaped ridges, so characteristic of modern ruminants. An example of primitive, possibly transitional, ruminants is seen in the extinct family of the *oreodonts* ranging in time from the Upper Eocene to the Upper Miocene and confined to North America; these were very numerous, not larger than a sheep, with four functional toes

upon each foot and a very long tail; the genus Oreodon is confined to the Oligocene. The family of *camels* (camels, llamas, etc.) originated upon the continent of North America from primitive Upper Eocene forms, and were confined to this continent through the Miocene. They were very abundant here during the Oligocene and Miocene. During the Pliocene they migrated into South America, Asia, and Africa, where they exist to the present, but they disappeared from their native home during the Pleistocene.

In the following forms — the true ruminants — the upper incisors are always absent, and likewise usually the upper canines. North America played a very insignificant rôle in the evolution of these forms. In the *solid-horned ruminants* (*e.g.*, deer) the usually branched horn, an outgrowth of the frontal bone, is shed each year; it usually increases in size and number of branches with each renewal. The deer family has been present in the Northern Hemisphere since the Miocene (Fig. 196, 3). They attained their maximum development in the Pleistocene and present. The giraffes (Pliocene to present), now confined to Africa, were formerly present also in Eurasia; they never had any representatives in the Western Hemisphere. In the *hollow-horned ruminants* (antelopes, sheep, oxen, etc.) the unbranched horn covers a solid bony outgrowth of the frontal bone; it is usually present in both sexes and is never shed, except in the pronghorn antelope of western North America, which species is similarly exceptional in having branched horns. The sheep (Ovis) and goat (Capra) are known from the Pleistocene of Europe. Domestic cattle (Bos) have been found in Asia from the Pliocene, in Europe since the Pleistocene, brought in by man, and in America since recent times only. The bison is known from the Pleistocene to the present in North America and Europe. The solid-horned and the hollow-horned ruminants diverged from a common stock in the Oligocene. Many of these wild ruminants, such as the deer and the bison, formerly threatened with extinction are now, under the protective laws prevailing in the United States and Canada, increasing in numbers.

Order 9. Sirenia (Sea Cows)

Aquatic mammals, with a moderate-sized head, a fish-like body, front limbs paddle-like, hind limbs absent, and a horizontally expanded tail fin. Bones solid, dense, heavy. Pelvic bones vestigial.

This order of sea cows, a highly modified offshoot of the ungulates, is probably of African origin. It is first recognized from the Eocene of Egypt and the West Indies; later it occurs also in Europe and America. During the Pliocene and Pleistocene it was abundant upon both the Atlantic and Pacific coasts of North America. At present it is represented by the dugong of the Indian Ocean and the manatee of the rivers of northeastern South America and western Africa. The sea cows and the elephants may possibly have a similar origin, both being derived from a form closely allied to the mid-Eocene Mœritherium (Fig. 201).

Order 10. Cetacea (Whales)

Aquatic mammals, with a large head, fish-like body, front limbs paddle-like, hind ones absent, and a horizontally expanded tail fin. Bones spongy, light. Vestiges of pelvic bones present.

These are probably descended from the unguiculates, or ungulates. They include:

1. Archeoceti (Zeuglodontia) — primitive Eocene whales with certain characters which are transitional to primitive Carnivora. The typical genus Zeuglodon has been found in the Eocene of eastern North America, Europe, North Africa, and South Australia.

2. Odontoceti — toothed whales, including (*a*) squalodonts, confined to the Tertiary; (*b*) dolphins, porpoises, etc., not known in the fossil state; (*c*) narwhals, not known in the fossil state; (*d*) sperm and beaked whales. Miocene to the present.

3. Mystacoceti — whale-bone whales, including the gray, fin, hump-backed and right whales, and the rorquals — are known from the Miocene to the present.

Order 11. Primates (Lemurs, Monkeys, Man)

Arboreal, or bipedal walking mammals, with thumb and often great toe opposable to the other digits. Digits usually five and provided with flat nails, very rarely with claws. Eye surrounded by a complete bony ring.

The primitive forms of the Primates are related to the Insectivora of the unguiculate section of mammals. Suborder (1) Lemuroidea (Lower Eocene to present) includes the extinct families Adapidæ (Notharctidæ) and Anaptomorphidæ, both Eocene of North America and Europe. The surviving family of Lemuridæ, the lemurs, has been found in the fossil state only since the beginning of the Pleistocene.

Suborder (2) Anthropoidea (Oligocene to the present) includes (*a*) the " broad nostril " or New World monkeys of South America to Mexico ; examples of these are the marmosets, not known in the fossil state, the capuchins, the howlers, spider and squirrel monkeys, some of which are known as fossils from the Pleistocene ; (*b*) the " narrow nostril " or Old World monkeys, the anthropoid apes, and man.

The Old World monkeys include the Indian and African monkeys, the baboons, macaques, and langurs. The anthropoid apes (family Simiidæ) include the extinct Propliopithecus (Lower Oligocene) of Egypt, Pliopithecus (Miocene), and Dryopithecus (Upper Miocene to Lower Pliocene) of Europe, and the four living anthropoid apes, the gibbon (Hylobates), the orang-utan (Pongo or Simia), the gorilla (Gorilla), and the chimpanzee (Anthropopithecus). Finally the family Hominidæ, or man, includes such extinct genera as Pithecanthropus (upper Pliocene or lower Pleistocene) of Java, Eoanthropus of similar age from Piltdown, England, Sinanthropus (the Pekin man) of lower Pleistocene or uppermost Pliocene age, from China. The genus Homo includes, among others, the extinct species *H. heidelbergensis* (lower Pleistocene) from Heidelberg, Germany, *H. neanderthalensis* (or *primigenius*), widespread in Europe and Asia during middle and upper Pleistocene, *H. rhodesiensis* (age

doubtful), found in the Broken Hill mine in Rhodesia. The species *H. sapiens*, which includes all living men, is well known from many fossil remains from the upper Pleistocene to the present.

1. Define Mammalia. What is the significance of the name?
2. What are the placental mammals? Why so called?
3. In what ways do the mammals represent an advance upon the reptiles? Your reasons?
4. Into what various habitats have mammals diverged?
5. Since the beginning of the Tertiary thousands of species of mammals have become extinct and many others have disappeared from a former habitat. Give some probable causes of such extinction, especially during (*a*) the Pliocene and (*b*) the Pleistocene.
6. Show that the three subclasses of the mammals represent an ascending series.
7. Enumerate the orders of mammals, giving a living and a fossil example of each where possible, and the significance of the names.
8. Give the geologic range of the Monotremata; the Marsupialia.
9. What marsupials exist outside the Australian region? Where? Why is the American opossum called a living fossil?
10. Define Cheiroptera, giving geologic range.
11. What are the Carnivora? Distinguish their three divisions, giving an example under each, stating likewise the geologic range of each.
12. How are rodents distinguished? Give the significance of the name; the geologic range.
13. Under what order has Glyptodon been placed? Why?
14. Define the order Ungulata. Distinguish them from Unguiculata.
15. In what part of the Tertiary were the hoofed and clawed mammals very similar in appearance?
16. What were the primitive Ungulata like? The incoming of what food aided largely in their separation into browsing and grazing types?
17. Enumerate the eight suborders of ungulates with an example and the geologic range of each.
18. Give briefly the evolution of the elephant. Distinguish between archaic and modern characters.
19. Describe the most conspicuous species of elephant in North America during the Upper Tertiary and Pleistocene.
20. How is the migration of animals brought about? How does the present distribution of a form give us knowledge of former geographic conditions?

21. Distinguish between the tooth of a true elephant (Elephas) and that of the more primitive mastodon.
22. What suborder of ungulates in South America paralleled the horses in their development? In what respects?
23. What is the significance of the name Perissodactyla? Why applied to this suborder?
24. Briefly trace the evolution of the horse. Upon what continent did this probably occur?
25. Make sketch to show why the horse's tooth (also elephant's tooth) is so well adapted to grinding hard grasses.
26. What genus of Perissodactyla was one of the largest of ungulates?
27. What is the significance of the name Artiodactyla? Why applied to this suborder?
28. What are the least modified descendants of the Artiodactyla? Why?
29. Why is it thought that the Lower Tertiary representatives of this suborder did not chew the cud?
30. Distinguish between the molar teeth of the horse and those of a ruminant like the cow.
31. What difference between solid-horned and hollow-horned ruminants? Give examples of each. When were these groups probably united?
32. When and upon what continent did the evolution of the camels take place?
33. What are sea cows? Their probable origin?
34. Name the three classes of whale, with an example of each. From what forms may they possibly be descended?
35. Define the order Primates. Give the suborders into which they are divided, with an example and the geologic range of each.
36. What is the difference between "New World" and "Old World" monkeys? Give examples of each.
37. Name the living anthropoid apes.
38. Give in geologic succession (*a*) genera of Hominidæ, (*b*) species of Homo.

Evolution of the Chordata

The origin of the chordates is still obscure. Many scientists have derived them from the annelids, others from the echinoderms, nemertines, flat worms, or arachnids. Their derivation from an early segmented, annelid-like stock appears to be indicated in the symmetrical arrangement of the muscles in

Amphioxus, the ostracoderms and the lamprey, as well as in the embryo of the shark, etc. Their derivation from the ancestral echinoderms is suggested by the bilaterally symmetrical larva, Tornaria, developed both by the members of this phylum and by the Enteropneusta; that is, under this hypothesis the Tornaria-like ancestor gave rise to the echinoderms in the direction of fixation and to the vertebrates in that of freedom. Whatever the pre-chordate ancestry, the most simple living chordates which thus give some conception of one of the earliest phylogenic stages are the Enteropneusta. The members of this subphylum have a very short notochord, gill-slits, and four longitudinal nerve cords, the dorsal one being more pronounced than the ventral and lateral ones. The notochord is the embryonic backbone, present in all of the chordates.

A succeeding stage appears to have been the ancestor of the tunicates. The present tunicate embryo, about a quarter of an inch long, looking much like a frog tadpole, has a notochord confined to the tail, gill-slits opening from the pharynx, and a primitive spinal cord extending dorsally throughout the body and ending anteriorly in an enlargement which is considered the forerunner of the brain of the vertebrates.

The next stage may be represented by the ancestors of the living degenerate Amphioxus, in which an advance is seen over the preceding in having the notochord extend throughout the body.

The ostracoderms gave rise apparently to the jawless lampreys and the jaw-bearing sharks. This extinct class agreed with the living cyclostomes in having the fundamental divisions of the brain seen in the vertebrates.

In such sharks as the Devonian Cladoselache, the upper and lower jaws have appeared but they are very primitive since they are in series with the gill arches. Paired fins have also just arisen from balancing fin folds (Fig. 176). Such fin folds had wide bases and limited mobility. From such primitive vertebrates descended the various groups of elasmobranchs of to-day and the early ganoids.

In the early ganoids is seen the evolution of the pectoral and

pelvic fins to more freely turning paddles. In the lobe-finned fishes of the late Devonian, the fins have internal supports corresponding to the bones in the limbs of the land vertebrate. In a living representative, Polypterus, is seen how readily these lobe-finned paddles may be directed downwards on either side of the body, in a position to assist in wriggling on the mud. The beginnings of such bones of the higher vertebrates as the frontals and parietals are seen in the enamel-covered bony armor over the head of the early ganoids. The ganoids are also characterized by the possession of a primitive lung, an outpocketing of the pharynx. This became the air-bladder or float of the higher fish and the lung of land vertebrates. From such early ganoids descended along different lines the true teleost fishes, the lung-fish and the amphibians.

Amphibia probably evolved during the Devonian under such semi-arid conditions as similarly gave rise earlier to the ganoids and the lung-fish. The annual drying up of pools formed by rivers overflowing their banks would give the necessary impetus to plastic individuals for a greater use of the lungs. Thus gradually through successive generations their vesicular structure developed, accompanied by the resorption of the more and more useless gills. At the same time the pectoral and pelvic fins, basically limb-like (Fig. 177), would be used for passing from dried-up pools to the rivers. They thus became more and more like true limbs for support and progression, developing a sharp angulation at knee and ankle, while the rays became modified to serve as fingers.

In the development of vesicular lungs and limbs capable of progression upon land, amphibians made a great stride in the evolution of dry-land animals. Since, however, they did not acquire the means of preventing a rather free evaporation of water from within their bodies, they must confine their activities to margins of pools or shady land areas near enough to pools to return for egg-laying. The primitive amphibians radiated into various lines, including the tailed and tailless orders of present-day amphibians and the early reptiles.

All land-living animals continue to be water inhabitants or rather inhabitants of water modified by the addition of salt and albuminous material, *i.e.*, the blood plasma. Protoplasm, the only living substance, can perform its functions only when it is moist. About two-thirds of the weight of man is water. Hence land animals surround themselves with a layer of dead or inert material. All the vital mechanisms of the body have only the object of preserving constant the conditions of life in the internal environment.

The reptiles eliminated the aquatic stage of the embryo by inclosing an artificial watery environment within an egg shell. They also developed a protection of dry horny scales against a rapid loss of water from their bodies. They were thus enabled to leave the neighborhood of water bodies and invade permanently the drier land of the earth. Since this, as well as the air, was unoccupied by any other vertebrates or large invertebrates, they could easily radiate into the varying habitats found there. And with their more highly evolved brain and body, they could also easily compete with the animals in the water. The primitive reptiles thus evolved into a great many orders, including the turtles, crocodiles, and snakes of to-day, as well as the birds and mammals.

The typical reptile is still cold-blooded and hence must surrender its active existence during cold weather. As the cold increases, the heart beats more slowly and the respiration becomes more infrequent until it practically ceases. When warmed up, the organs work again. For many of the essential processes in organisms are chemical and the speed of chemical reactions varies with the temperature. Thus the cold-blooded reptile would be at a disadvantage during colder periods — the nights and the winters — over warm-blooded animals. The evolution of the heart may be traced from the simple tube of Amphioxus through the two-chambered organ of the fish, the three-chambered of the amphibians, and the incompletely four-chambered one of the reptiles, to the completely four-chambered heart of the birds and mammals. The heart of

existing reptiles is nearly fitted to produce a uniform high temperature; it is as yet impossible to state to what degree this stage had been attained by various orders of extinct reptiles.

The derivation of birds and the bird-like dinosaurs from apparently the same carnivorous dinosaur ancestors possibly tends to indicate an at least partial warm-bloodedness for the latter also. The former took to a life in the air, the latter to one upon land. Despite this difference in habitat, both developed many features in common — foot and pelvic bones, the tendency to use only hind legs in walking, a trend towards the loss of teeth, and the development of horny beaks. In birds the scales developed into feathers, a change which can be seen on the legs of birds to-day. These feathers aided in the maintenance of a uniform high body temperature.

Somewhere along the line leading to the mammals, hair was developed as a covering accessory to that of scales. In many orders of mammals to-day, such as marsupials, insectivores, and rodents, hairs grow at the sides and front of the imbricating scales, thus outlining the scale. The hairs over the rest of the body are arranged according to this pattern. The evolution of hair would be an aid to the maintenance of a uniform and high body temperature.

Leading up to the mammals were the progressive cotylosaur and theromorph reptiles of the late Paleozoic. The South African theromorphs had begun to lift the body off the ground by bringing the legs beneath the sides of the body and straightening the knees' angulation. In the Triassic of the same region appeared the cynodonts. These are intermediate between primitive reptiles and typical mammals. The skeleton is well fitted for running and the skull is strikingly like that of a primitive mammal in the arrangement of its various bones. The teeth are divided into incisors, large canines, and molars instead of the typical reptilian series; the lower jaw too was composed of one large bone, the dentary, and several small ones, instead of the dentary alone as in the mammals or of all small bones as in

typical reptiles. It is impossible to say how far the cynodont reptiles had traveled towards the maintenance of a high body temperature. In the lowest order of existing mammals, the monotremes, the body temperature is still quite variable, rising or falling as much as 15° F. according to the surrounding temperature. These show an additional close reptilian affinity in laying eggs, and their mammary glands are most primitive in lacking nipples. The next higher order, the marsupials, are intermediate between these and the true placentals which include all other mammals. The various orders of the placental mammals represent distinct radiations from these generalized ancestors into various habitats and adaptations to different types of food. Upon the lands, the ungulates feed upon grass and twigs, the rodents upon nuts and bark, the carnivores upon flesh, while the primates tend towards an upright posture, and the edentates, becoming degenerate in tooth structure, vary in many ways. The bats take to a life in the air and the Sirenia and whales to the ocean, the former upon the margins and the latter far from land.

Vertebrates as rock-builders. — The bones of vertebrates and the excrement (guano) of, especially, carnivorous animals (fish, reptiles, birds, bats) collect at times in sufficient quantity to make up a comparatively large percentage of the mass of strata. Such resultant phosphate deposits are known at intervals from the mid-Paleozoic to the present. The phosphorus in the bones comes originally from igneous and crystalline rocks, generally from apatite. Apatite is dissolved by waters holding CO_2, especially when humus acids are also present. Some of the phosphoric acid is carried by streams to the ocean where certain plants and invertebrate animals utilize it, not only in their living tissues as must all life, but also in building their skeletons. Inarticulate brachiopods, copepods, and decapods are especially noteworthy in this respect. The phosphates retained in the soil are taken up by the roots of land plants. From the small amount of phosphorus in these organisms the vertebrates derive the large amount needed for their skeletons.

1. Divide the phylum Chordata into subphyla, classes, and all minor subdivisions, giving an example of each.
2. Distinguish the Chordata from Invertebrata.
3. Why is the name Chordata used for this phylum?
4. Which alone of the four subphyla has known fossil representatives?
5. What is the significance of the term Vertebrata for the members of this subphylum?
6. Name the phyla into which animals are divided, giving the bases of this classification. How does this increase in complexity of organization correspond to the order of their appearance in geologic time?
7. Briefly outline the evolution of the chordates.
8. Discuss vertebrates as rock-builders.
9. Whence do vertebrates derive the phosphorus for their bones?

INDEX — GLOSSARY

Every reference is to the page; words in italics are names of genera and species. Figures in italics indicate illustrations; in heavy type principal descriptions.